

THE EVOLUTION OF THE MAMMALIAN EARDRUM AND TYMPANIC CAVITY

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INTRODUCTION

Two opposite views on the origin of the mammalian middle ear have been expressed by Gaupp (1913) and Goodrich (1930). Gaupp held that the eardrum of reptiles was essentially supramandibular and that of mammals submandibular, so that the latter could not have arisen from the former, but must have evolved separately. Goodrich, on the other hand, declared that the tympanic membrane, middle ear cavity and Eustachian tube in reptiles and mammals were completely homologous with one another. Recently, as more has been discovered of the anatomy of mammal-like reptiles, it has become clear that the tympanic membrane is situated more antero-ventrally in mammals than in reptiles, but it is not immediately apparent at what stage the migration occurred. Watson (1953) emphasized how undesirable it would be to suppose that the change was 'saltatory', that is to say, that it involved some major jump or discontinuity in evolution. Nevertheless, he himself was led to the conclusion that in some of the synapsid ancestors of mammals the eardrum was completely lost. He based this view on the large size of the stapes, its extensive contact with the quadrate, and the lack of an obvious site for an external auditory meatus in certain members of the captorhinomorph-pelycosaur line. Below the skin, however, the original middle ear cavity supposedly remained in communication with the pharynx (this sometimes happens, though not usually, in those lizards in which the external auditory meatus and tympanic membrane have been lost), and contact with the surface was re-established in therapsids to form a new tympanic membrane and a new external auditory meatus.

Westoll (1943), and other workers, have not believed that synapsids lost and redeveloped their tympanic membranes. According to Romer & Price (1940), pelycosaurs could have possessed an eardrum, sunk as in many lizards in the depths of an external auditory meatus, between the quadrate in front and the depressor mandibulae muscle behind. Parrington (1946, 1955) showed that such a drum could have been present in cynodonts and gorgonopsids.

The problem is to explain how an eardrum originally in the reptilian position could come to be embraced by the mammalian ectotympanic bone. Gaupp (1911*b*) originally homologized the ectotympanic of mammals with the reptilian angulare, and Palmer (1913) noted the resemblance between the ectotympanic of the marsupial *Perameles* and the reflected lamina of the angulare in late cynodonts. Consequent upon their observations, it has been generally agreed that at some stage during synapsid evolution the periphery of the tympanic membrane must have reached the angulare. In spite of this, Romer & Price have demonstrated that the reflected lamina could not always have supported an eardrum. Their arguments were that

migration of the drum forwards from the reptilian site would have been prevented by the depressor mandibulae, that the stapes could not have been connected to a drum in this position, that there would often not have been room for a tympanic cavity deep to the drum, that it would have been obstructed by pterygoid muscles, and that a tympanic membrane so far forward would have interfered with movements of the lower jaw.

Some of these difficulties were met, and the awkward gap between synapsids and mammals bridged, by a theory of the evolution of the middle ear devised by Westoll (1948). Sushkin (1927) had already concluded that part of the *cavum tympani* in mammal-like reptiles generally must have approached the surface below the jaw articulation, to form a drum in the notch of the *angulare* which, he believed, was represented to some extent even in early forms. Westoll postulated that a diverticulum, 'either originally separate from the Eustachian tube and tympanic cavity, or much more probably an extension of the tympanic cavity itself', grew out to meet the *angulare* and eventually became supported by it. A similar suggestion had been made by Watson (1951) in his original Silliman lectures. Westoll gave this diverticulum the name '*recessus mandibularis tympanicus*', and illustrated its position in a pelycosaur, a cynodont and a thercephalian. He thought that its original function might have been to act as a resonator comparable to the vocal sacs of frogs, and that eventually its outer wall approached the skin surface around the retro-articular process of the *articulare*, which then became transformed into the *manubrium mallei* of a true eardrum of mammalian type. Later (1945), Westoll clinched his theory by homologizing Shrapnell's membrane, that is, the *pars flaccida* of the mammalian drum, with the original tympanic membrane of the ancestors of mammals, and with the eardrum possessed by modern reptiles. He interpreted the malleolar folds between the *pars flaccida* and the *pars tensa* as 'the reduced and compressed equivalent of the tissues which laterally separated the upper part of the tympanic cavity of therapsids from the *recessus mandibularis*'.

Westoll's interpretation is a neat one, and has received very general acceptance, notably from Parrington (1949) and Gregory (1951). Parrington later (1955) expressed some doubts whether a diverticulum of the tympanic cavity could act as a resonator. Vaughn (1955) also accepted most of Westoll's conclusions, but pointed out that his theory did not explain the course of the *chorda tympani*, which runs dorsal to the tympanic membrane of reptiles and ventral to Shrapnell's membrane in mammals. Vaughn attempted to resolve this difficulty by reference to skull morphology. He supposed that, as a result of changes in the proportions of the temporal region occurring in the early stages of synapsid evolution, the middle ear and its contents were 'driven ventrally', and 'drove the *chorda tympani* before them'. Later the *recessus mandibularis* pushed out ventrally, and the *chorda tympani* was trapped between it and the original tympanic cavity.

The purpose of the present paper is to draw attention to certain problems which the hypothesis of a *recessus mandibularis tympanicus* does not solve, and to put forward as an alternative a theory, supported by some evidence, which is in line with Westoll's other suggestion of a pharyngeal diverticulum distinct from the Eustachian tube.

PRESENT THEORY

A strong argument, based on morphological considerations, against the view that the mammalian middle ear has evolved from a diverticulum of the original tympanic cavity, is that it does not account for an apparent antero-ventral shift in mammals, not only of the tympanic membrane but also of the opening of the Eustachian tube. Evidence of this change in position is as follows. First, the tubotympanic recess in mammals approaches the auditory ossicles from in front, with, above it, the internal carotid artery *leaving* the region of the middle ear. In reptiles such as lizards, on the other hand, the Eustachian tube runs laterally from the pharynx, and the internal carotid *approaches* the tympanic cavity in its roof (Figs. 2, 3B, 5A). Secondly, the fenestra rotunda, bearing the secondary tympanic membrane, overlies the Eustachian tube in lizards, whereas in mammals it is in the roof of the extreme posterior cul-de-sac of the tympanic cavity, as far away as could be from the Eustachian tube. Thirdly, it is generally agreed that the tensor tympani of mammals is a transformed muscle of mastication, derived from the reptilian adductor mandibulae internus (= anterior pterygoid, pterygo-mandibularis). In reptiles the adductor mandibulae internus is ventral to the Eustachian tube (Fig. 3), and Westoll (1943) accordingly showed it in this position in his figure of the recessus mandibularis in a cynodont. In mammals, however, the tensor tympani runs in the upper part of the tympanic cavity (Fig. 5A), and its origin is dorsal to the Eustachian tube. The tensor palati muscle presents similar difficulties.

Parrington & Westoll (1941) have shown that during synapsid evolution the anterior part of the basis cranii has undergone shortening. It is doubtful whether this can account for the changed relations of the Eustachian tube, since the latter opens behind the basiptyergoid process, while the shortening apparently occurs in front of it. It seems, therefore, that the concept of a tympanic diverticulum may explain some, but cannot explain all, of the features of the mammalian middle ear. Furthermore, it does not receive direct support from embryology. Ontogeny, of course, is not obliged to repeat the stages of phylogeny, but an *ad hoc* postulate of this sort would gain in plausibility if some indication of its occurrence could be seen during embryonic development. One might, for instance, expect to find in mammalian development the tubotympanic recess first growing out around the primordium of the stapes, since it is the oldest ear ossicle; and later a pouch being thrown out towards the ectotympanic which would envelop the handle of the malleus. In fact, however, no such pouch is formed, and the tubotympanic recess meets the manubrium mallei first of all (Fig. 1), reaching the stapes and the attic region of the middle ear only at a relatively late stage (Fig. 5A). This is a constant finding in eutherian mammals, and is in accordance with McClain's observations (1939) in the marsupial *Didelphys*. Similarly, unless there has been a reversal in the order of events during ontogeny, Shrapnell's membrane as an ancestral reptilian heritage should make an early appearance. Actually, it seems to be the very last part of the eardrum to develop, not appearing in man until the final month of foetal life (Keibal & Mall, 1912).

Further objections to the theory that the tympanic cavity acquired a mandibular recess during phylogeny are the following. First, it is not clear what would have

been the original purpose of such a recess. Why should a diverticulum have grown out from the tympanic cavity in the first place, meeting the angulare so conveniently for the subsequent formation of a pars tensa of the tympanic membrane? Although vocal resonators are common amongst modern tetrapods, there is no instance of one having been developed from the middle ear. The vocal sacs of frogs are not of tympanic origin, but are formed as diverticula of the buccal cavity. Secondly, it seems curious that a simple outpouching of the tympanic cavity should exert such forces during morphogenesis as to entrap the chorda tympani and compress the tissue of the malleolar folds. Thirdly, an extension of the middle ear attached to the lower jaw, even before the development of a tympanic membrane, would probably have been something of an embarrassment both to mastication and to hearing.

In the light of these difficulties, it was felt that an alternative explanation must be sought to interpret conditions in mammal-like reptiles and to account for the

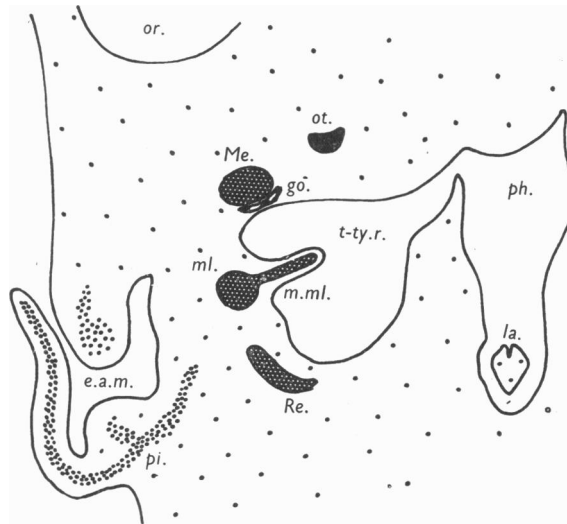


Fig. 1. *Elephantulus* embryo, 14 mm. Section showing the typical mammalian relation of the tubotympanic recess to the manubrium mallei.

differences between the Eustachian tube, middle ear cavity and tympanic membrane of modern reptiles and mammals. The middle ear and pharyngeal regions were studied, therefore, in a number of lizards, to see whether any clue could be obtained as to how the tympanic cavity and membrane of mammals might have evolved. This was done with the realization that only those features could be relied on which might reasonably be considered primitive and to have been present also in early mammal-like reptiles. In fact, the lizard ear, compared with that of other modern reptiles such as turtles and crocodiles, appears to retain in most respects a relatively simple organization. The Eustachian tube communicates directly with the pharynx as in the embryo (Fig. 2); the position of the tympanic membrane behind and below the quadrate and above the retro-articular process of the articulare is similar to its presumed site in pelycosaurs and other primitive synapsids; and Westoll (1943) and Parrington (1955) have shown that the cartilaginous processes of the extra-

stapes, which are so prominent in lizards, have their equivalents in all tetrapods, living and extinct.

It was found that in lizards, in front of the opening of each Eustachian tube and at a somewhat lower level, there is a lateral extension of the pharyngeal cavity which forms a deep groove on each side below the jaw (Fig. 3A). Embryologically this groove is formed as a recess of the hyoid pouch, antero-ventral to the precursor of the tympanic cavity, so that eventually it separates the skeletal elements, with their musculature, of the mandibular and hyoid arches. At its posterior end each groove fades out below the Eustachian tube, from which it is separated by the retro-articular process of the articulare and the attached adductor mandibulae internus muscle (Fig. 2). The lining epithelium of the groove consists of ciliated columnar

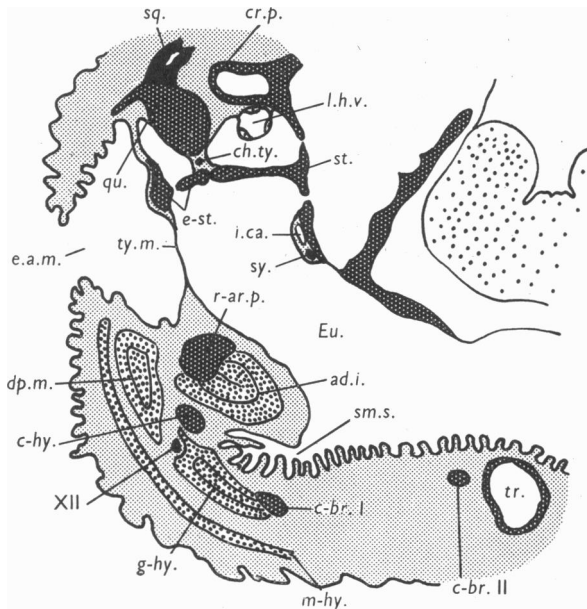


Fig. 2. *Acanthodactylus* post-natal. Transverse section showing middle ear structures in a lacertid lizard. The adductor mandibulae internus is ventral to the Eustachian tube and dorsal to the submandibular sulcus. The chorda tympani crosses the roof of the tympanic cavity.

and goblet cells and is arranged in folds similar to that of the floor of the pharynx and oesophagus adjoining it. Deep to the epithelium are many capillaries derived mainly from the tracheo-laryngeal branches of the pulmonary arteries, which also supply the pharyngeal floor. It is proposed to call this lateral extension of the pharynx the *sulcus pharyngis submandibularis*, or submandibular (pharyngeal) sulcus.

The appearance and relations of the submandibular sulcus are so like those of the developing tubotympanic recess of mammals (Fig. 3B), that there would seem good reason to suppose that, if such a structure were present in synapsids, it might well have played a part in the genesis of the mammalian middle ear cavity. The function of the submandibular sulcus in lizards is almost certainly to facilitate distension of the pharynx, particularly in the pulsatile movements which occur with pharyngeal

respiration. Drummond (1946) produced anatomical and experimental evidence that the pharynx and oesophagus, apart from assisting in ventilating the lungs, have themselves an active respiratory role in lizards, up to 10% of the resting CO_2 being eliminated across their walls. It is clear from Fig. 3A that, when the hyobranchial apparatus is raised by the geniohyoid and mylohyoid muscles, the walls of the submandibular sulcus will be opposed, but descent of the floor of the pharynx,

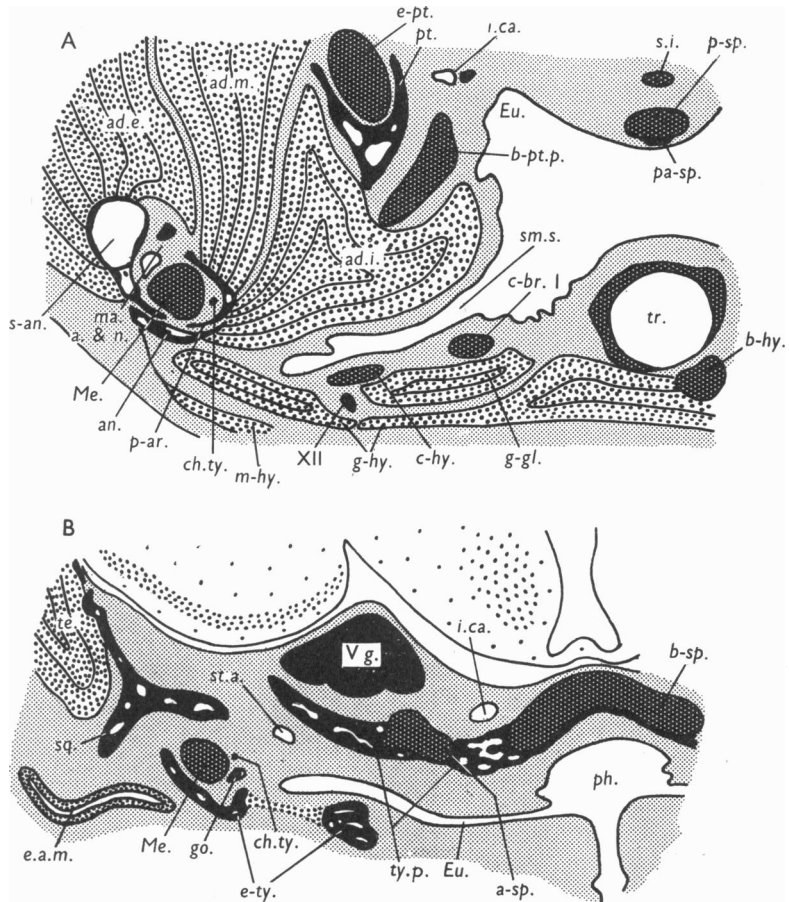


Fig. 3. (A) *Psammodromus* post-natal. Transverse section showing the relation of the submandibular sulcus to lower jaw structures in a lacertid lizard. (B) *Potamogale* embryo 16 mm. head length. Comparable transverse section through the Eustachian tube in an Insectivore. The ectochondral ossification below the basisphenoid and alisphenoid (tympanic process) is probably the equivalent of the reptilian parasphenoid.

necessarily accompanied by some unfolding or stretching of the subgular skin, will result in each sulcus opening out, thereby increasing both the volume of the cavity of the pharynx and the area of pharyngeal epithelium exposed to the air contained in it. This accessory respiratory mechanism may well have been utilized by early synapsids. Parrington (1934) suggested that the possession by some therapsids of a distinct thorax may have indicated that they had developed diaphragmatic

breathing. This would have enabled them to dispense with the less efficient methods required by their predecessors, and the submandibular sulcus could then be converted to other uses.

Some positive evidence that early mammal-like reptiles possessed a submandibular sulcus is provided by Sushkin's observation (1927) that in primitive (non-sphenacodontid) pelycosaurs and in captorhinomorphs there was a smooth, broad impression on the ventro-medial face of the back of the mandible. Sushkin believed that this impression received a diverticulum of the tympanic cavity, but it seems much more likely that it was caused by the submandibular sulcus, which could have made contact with any part of the back of the mandible not covered by muscle. It is significant that Sushkin also regarded the impression as an initial stage of the notch caused by the reflected lamina of the angulare which characterized all therapsids and advanced (sphenacodontid) pelycosaurs. A well-developed notch could hardly have failed to accommodate the submandibular sulcus, so long as the pterygoideus musculature (adductor mandibulae medius and internus) did not extend down on to the reflected lamina. Apart from its probable relation to the outer wall of the submandibular sulcus, which has not previously been realized, the reason for the existence of a reflected lamina has been disputed. Romer & Price (1940) supposed that its function was in fact to increase the insertion of the pterygoid muscles; Parrington (1955), on the other hand, associated it, in gorgonopsids at least, mainly with the masseter. If Romer & Price are correct in their interpretation, the submandibular sulcus could not have entered the notch of the angulare directly from the medial side, although it might perhaps have grown into it from behind.

Probably the reflected lamina of the angulare was first developed as a broad muscular process for the insertion of the masseter on its lateral surface, and incidentally supported the submandibular sulcus on the inner aspect of the notch. At some point, however, before the emergence of mammals, the masseteric attachment must have migrated forwards on to the dentary, leaving the angulare free. The reflected lamina then underwent reduction: in advanced cynodonts it formed a narrow bar somewhat medial to the body of the dentary. A similar reduction occurring in the actual ancestors of mammals would have permitted this vestigial muscular process to become a rudimentary ectotympanic. At the same time, the submandibular sulcus, now regressive as an organ of respiration, would have been available and suitable by virtue of its relation to the reflected lamina for conversion to the service of hearing. First, however, the outer wall of the sulcus must make contact with the surface. This would not have been difficult even if the old eardrum had disappeared as Watson believed, needing only that the mylohyoid and geniohyoid muscles should migrate forwards along the mandible (Fig. 2A). If, on the other hand, the reptilian drum was never entirely lost, contact could have been achieved by a downgrowth of its cuticular layer towards the submandibular sulcus in the depths of an external auditory meatus.

Could such an event have occurred during the history of cynodonts? An external auditory meatus is generally believed to have been present in the advanced cynodont *Gomphognathus*, in a deep groove at the back of the jugal process of the squamosal, and may have occupied a similar position, as Parrington (1955) has shown, in earlier therapsids. The groove in the squamosal may have partly lodged some type of

cartilaginous pinna, and its base marks the postero-superior limit of what would have been the attachment of the tympanic membrane—in *Gomphognathus*, immediately below the squamoso-quadrata articulation. A membrane stretching from here downwards and ventrally to the notch of the angulare, as reconstructed by Watson (1951, 1953), would have been fantastically large and unwieldy. It could not have contributed significantly to the transmission of sound by air-conduction via the articulare, whilst that bone still formed an integral part of the lower jaw; nor via the extra stapedial process, since the antero-inferior extension would have been cut off from the rest of the drum by the retro-articular process, and also by the depressor mandibulae which, according to Parrington (1955), was still present and inserted into the retro-articular process in *Gomphognathus*. More probably, the tympanic membrane in all cynodonts was a relatively small structure still occupying the primitive position opposite the outer end of the stapes, below and behind the quadrata, and above the retro-articular process of the articulare.

If these assumptions are correct, the mammalian type of tympanic membrane must have originated very late in therapsid history, little in advance of the establishment of a sound-conducting ossicular chain. Direct evidence of the process, therefore, is unlikely to be forthcoming until more is known of the anatomy of the ictidosaurs—the therapsid group transitional to mammals. In the present state of knowledge it is impossible to say more than that the mammalian drum, supported by a tympanic annulus, *could* have been formed as a result of the submandibular sulcus approaching either the skin surface or more probably the cuticular layer of the original tympanic membrane, and to indicate further changes in bony and soft tissues which would have led therefrom to the formation of the middle ear cavity and Eustachian tube of mammals.

Quite early in synapsid evolution the retro-articular process of the articulare tended to become deflected downwards, in connexion, as Parrington (1955) has argued, with the function of the depressor mandibulae. This, together with shortening of the postdentary portion of the mandible would have brought the angulare closer to the external auditory meatus, if present. Growth of the latter in a downwards and forwards direction, lateral to the retro-articular process, could have caused an extension of the cuticular layer to be applied to the outer wall of the submandibular sulcus, the two epithelia being supported circumferentially by the angulare and its reflected lamina. In this way, part of the drum would be brought below the level of the lower jaw (Fig. 4A). If by this time the depressor mandibulae had regressed or lost its original insertion, the old supramandibular and the new submandibular parts of the drum would be continuous below the retro-angular process. The extension might then have served to augment the conduction of sound to the extrastapedial process.

Externally, the enlarged drum would be formed by a single epithelial sheet, derived from the cuticular layer of the external auditory meatus; but its inner layer would be compound, being formed by the walls of the original tympanic cavity and the submandibular sulcus meeting on either side of the retro-articular process. After the regression of the depressor mandibulae these two diverticula could become continuous at their openings into the pharynx, below and behind the retro-articular process. They may have remained partly distinct so long as the articulare and

quadrate formed the functional jaw-joint. The original tympanic cavity could then continue to make hearing possible by enveloping the stapes and extrastapes, while the primary auditory purpose of the submandibular sulcus, which would have suffered from the disadvantage of moving with the lower jaw so long as the angulare was part of it, would be to contribute the mucosal layer to the new portion of the

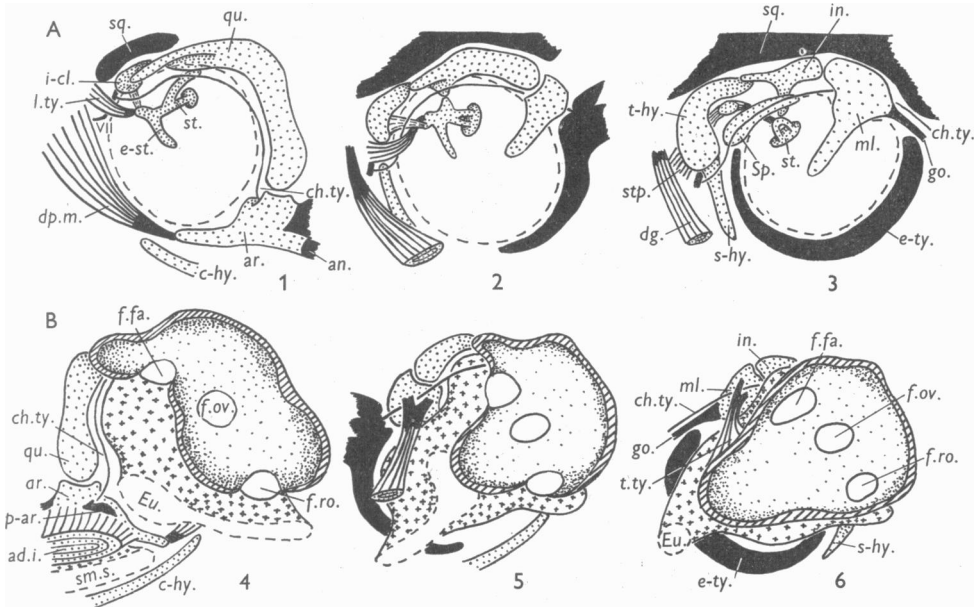


Fig. 4. Semi-schematic diagrams indicating how the mammalian middle ear could have evolved from a reptilian precursor. Membrane bones are shown black and chondral structures shaded with a dotted stipple. (A) Right ear, lateral view. The position of the tympanic membrane is marked by a broken line. (1) Lacertilian condition. The tympanic membrane is supported above and in front by the quadrate, below by the retro-articular process, and behind by the depressor mandibulae. (2) Hypothetical intermediate stage, with the extra-stapes retained, the articulare freed from the depressor mandibulae, and the tympanic membrane extending to the reflected lamina of the angulare. (3) Mammalian condition. Shrapnell's membrane (not shown) occupies the area above the chorda tympani, whose course relative to the tympanic membrane proper is unchanged. (B) Right ear, medial view, showing the cut outer wall only of the auditory capsule, and omitting the tegmen tympani and entotympanic. The mouths of the Eustachian tube and submandibular sulcus are marked by broken lines, and the walls of the tympanic cavity and submandibular sulcus are stippled with crosses. (4) Lacertilian condition. The Eustachian tube opens above and the submandibular sulcus below the retro-articular process and the adductor mandibulae internus. (5) Hypothetical intermediate stage, in which the submandibular sulcus has made contact with the tympanic membrane and has become confluent with the original tympanic cavity. (6) Mammalian condition. The narrowed Eustachian tube opens in the site of the former submandibular sulcus. The tensor tympani is shown with a double tendon embracing the chorda tympani, as in bats.

drum. Eventually, the two would form a common middle ear cavity, in which the articulare and quadrate become enclosed.

The partial closing off of this cavity from the pharynx was probably linked with the development of the cochlea. In the evolutionary line leading to mammals there must have been an improvement not only in sound conduction but also in the

perceptive apparatus of hearing, whereby the original papilla basilaris of primitive reptiles became greatly elongated to form an organ of Corti. To accommodate the latter, the pro-otic grew out antero-ventrally, and in so doing would occupy the space taken up by the wide mouth of the original Eustachian tube. In this way the tympanic cavity would acquire a new medial wall in the previously deficient lower

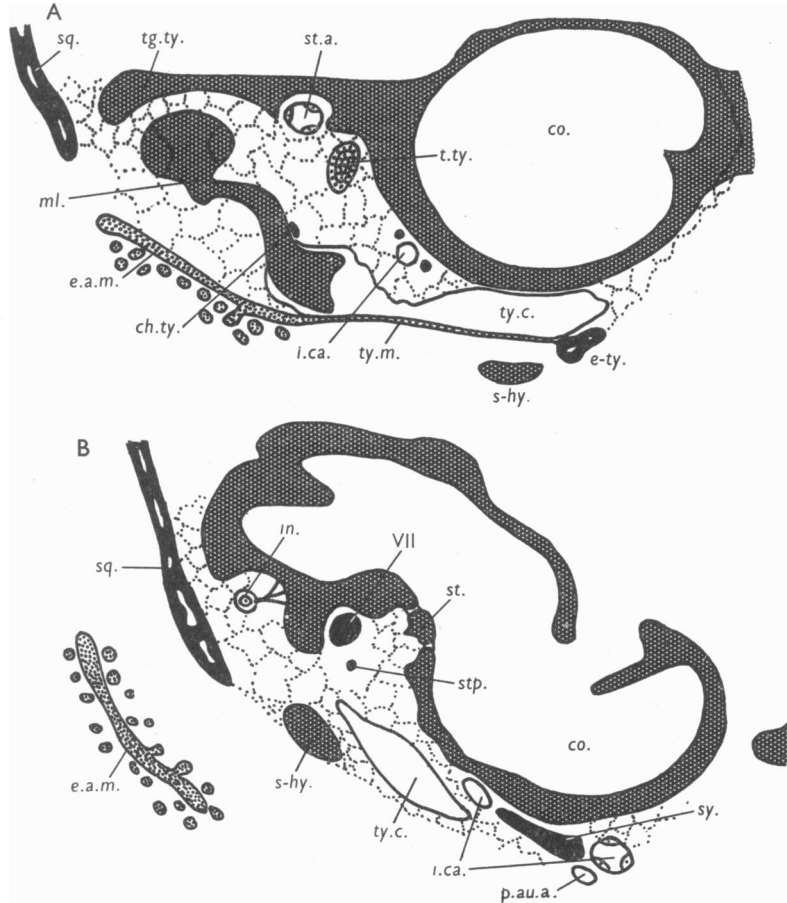


Fig. 5. *Elephantulus* embryo, 27.5 mm. Transverse sections showing middle ear structures in a primitive eutherian mammal. (A) Level of the malleo-incudal joint. The tympanic membrane is unattached along its latero-superior margin. The tympanic cavity has not yet invaded the attic region, which is filled by mesenchyme. (B) Level of the footplate of the stapes, behind the tympanic membrane, passing through the posterior tip of the tympanic diverticulum. The short process of the incus is seen in the fossa incudis. The internal carotid artery and the accompanying cranial sympathetic trunk are entering the middle ear.

part which communicated directly with the pharynx (cf. Figs. 2 and 5A). The original Eustachian tube would become obliterated, and the pharyngeal opening of the middle ear cavity be limited to the narrowed mouth of the submandibular sulcus, which would then represent the definitive Eustachian orifice of the naso-pharynx (Fig. 4B).

The mammalian middle ear, therefore, compared with its reptilian precursor, has an enlarged lateral wall due to the extension of the eardrum, and an enlarged medial wall due to the growth of the cochlea. It acquires a new roof from the tegmen tympani growing out from the periotic, and a new floor from the entotympanic. The membranous lining has, according to the foregoing argument, a twofold origin. The submandibular component, derived from the submandibular sulcus, forms the Eustachian tube and the part of the middle ear between the promontory of the cochlea and the segment of the drum below and in front of the handle of the malleus. The supramandibular component, derived from the original tympanic cavity, forms the rest of the middle ear chamber; it no longer connects directly with the pharynx, owing to the growth of the cochlea closing its medial wall, but communicates with the submandibular component below the handle of the malleus. Structures such as the secondary tympanic membrane and the carotico-stapedial arterial trunk, which were dorsal to the old Eustachian tube, find themselves in the roof of the tympanic cavity well behind the pharynx (Fig. 5B).

The following further modifications must occur to bring the middle ear to the full mammalian state. The retro-articular process, already in the position of a manubrium mallei, will take on its shape and function. The adductor mandibulae internus, now a tensor tympani and no longer a masticatory muscle, will occupy the roof of the new Eustachian tube, since that structure is morphologically a submandibular derivative. The angularis will be freed from the lower jaw and become applied to the squamosal. Further growth of its reflected lamina will cause it to give attachment, not only to the new extension of the drum, but also to the back of its original postero-superior part, which was originally supported by the belly of the depressor mandibulae. The transformation to an ectotympanic is then complete. Of the other postdentary membrane bones, the surangularis is probably lost or reduced to the occasional ossiculum accessorium mallei, and the pre-articulare converted to the anterior process of the malleus (see Discussion).

According to the present theory, the primitive eardrum of reptiles is represented in mammals not by Shrapnell's membrane but by the morphologically supra-mandibular portion of the pars tensa—that is, the segment behind and above the manubrium mallei. Shrapnell's membrane is regarded as a new formation in mammals—an upward extension of the drum proper which, with the squamosal, forms the lateral boundary of the attic region or epitympanic recess, accommodating the bodies of the malleus and incus. Behind the epitympanic recess is the fossa incudis, enclosing the short process of the incus: the latter is probably derived from the posterior flange of the quadrate, which originally supported the tympanic membrane from above (Figs. 4A, 5B, 6). The epitympanic recess is partially separated from the rest of the middle ear chamber by the anterior and posterior malleolar folds. These form inward projections of the mucosal layer of the drum, and may be relics of the process by which the articulare and quadrate became incorporated into the tympanic cavity. The posterior malleolar fold corresponds in position to the outer part of the roof and anterior wall of the reptilian middle ear, formed by the quadrate. On this interpretation, the chorda tympani has not changed its course relative to the tympanic membrane during the evolution of mammals. Its relation to the posterior malleolar fold between the back of the pars tensa and

Shrapnell's membrane is the precise mammalian equivalent of its situation in lizards, below and behind the quadrate in the roof and anterior wall of the middle ear (Fig. 2).

The chorda tympani in reptiles retaining a middle ear runs dorsal to the cartilaginous extrastapes. In mammals, where an efficient sound-conducting apparatus is provided by the malleus and incus, a direct connexion between the stapes and the eardrum is no longer desirable: the extrastapedial process accordingly becomes vestigial, or perhaps disappears. It is necessary in this respect to consider the status of the cartilages of Paauw and Spence which, although commonly regarded as extrastapedial remnants, have given rise to some controversy. These small elements chondrify much later than other middle ear structures, and do not appear to occur

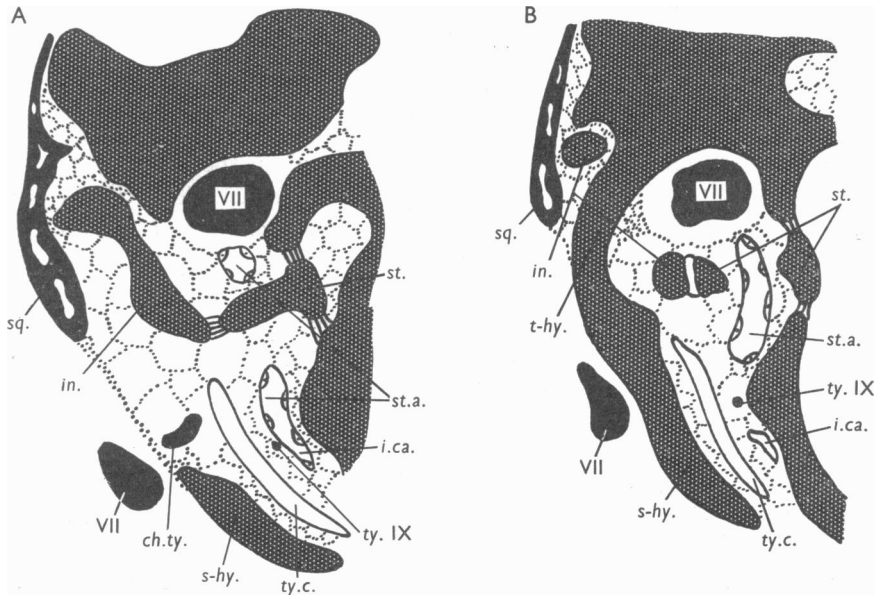


Fig. 6. *Potamogale* embryo, 16 mm. head length. Transverse sections illustrating the formation of the fossa incudis between the squamosal laterally and the tympanohyal medially. In (A) the chorda tympani is hooking round the stylohyal, and in (B), which is more caudal, the stapedial artery is piercing the stapes.

in every mammalian group. Paauw's cartilage, situated in the tendon of the stapedius muscle, has not been found in Insectivora. Spence's cartilage is laid down in mesenchyme adjacent to, and partly enclosing, the chorda tympani as it follows the posterior malleolar fold (Fig. 7A). McClain (1939) did not report it as such in *Didelphys*, but described a cartilage lateral to the malleus which he homologized, tentatively and most improbably, with the membranous surangulare. His account and figures suggest that this structure may have been the cartilage of Spence.

Olson (1944), following van der Klaauw (1923), regarded Spence's cartilage as homologous with the processus internus or quadrate process of the stapes. Westoll (1944) rejected this view, on the reasonable grounds that the point of contact between the stapes and quadrate is likely to have remained constant, so that the processus internus must form the head of the stapes in mammals. He considered

Spence's cartilage to be equivalent to the 'distal (tympanic) portion' of the extrastapes—that is, the processus inferior, and Paauw's cartilage to the 'proximal', horizontal or hyostapedial portion. Findlay (1943) had previously identified the latter with Spence's cartilage, and the processus inferior with the manubrium mallei. Findlay's view, as Westoll pointed out, is at variance with the strong embryological and palaeontological evidence for regarding the manubrium mallei as a derivative

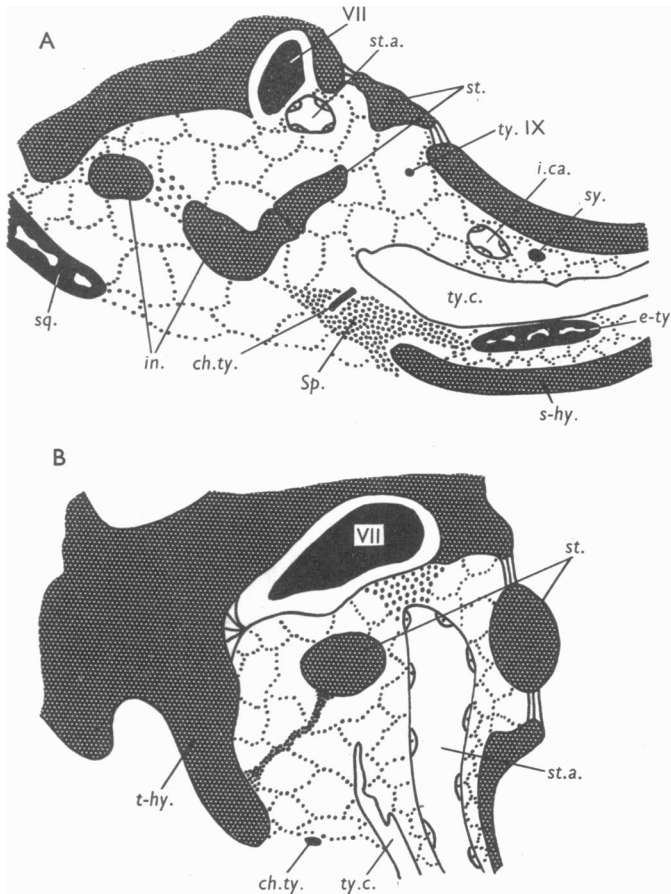


Fig. 7. (A) *Elephantulus* embryo, 27.5 mm. Transverse section showing the posterior end of Spence's cartilage at a blastemata stage, forming around the chorda tympani. Spence's cartilage was chondrified in a 47 mm. embryo of *Elephantulus*. (B) Neonatal mouse. Transverse section showing the occurrence of a ligamentous connexion between the stapes and the tympanohyal.

of Meckel's cartilage and equivalent to the retro-articular process of the articulare. On the other hand, Westoll's interpretation, although fitting the general position of the cartilages, has the disadvantage of requiring the extrastapedial process to have been fragmented into two pieces while failing to explain the associations of the fragments with the stapedius muscle and the chorda tympani.

In those reptiles which have lost the tympanic membrane, the stapes becomes firmly fixed to the quadrate and the extrastapes disappears. If, then, the cartilages

of Paauw and Spence are indeed extrastapedial vestiges, their persistence in mammals is evidence against the tympanic membrane having been lost and reformed in ancestral synapsids. It is by no means certain, however, that these elements are atavistic structures. Since the Eustachian cartilage seems to have been developed by mammals with no known reptilian precursor, it is possible that the cartilages of Paauw and Spence should also be regarded as mammalian specializations, and their late appearance in ontogeny would support this view. The significance of each may be functional rather than morphological: Paauw's cartilage acting as a sesamoid, and Spence's cartilage supporting the upper part of the pars tensa of the tympanic membrane.

If, on the other hand, the cartilages of Paauw and Spence do represent parts of the reptilian extrastapedial apparatus, they must be considered in terms of the comparative embryology of the hyoid arch skeleton. In early embryonic stages

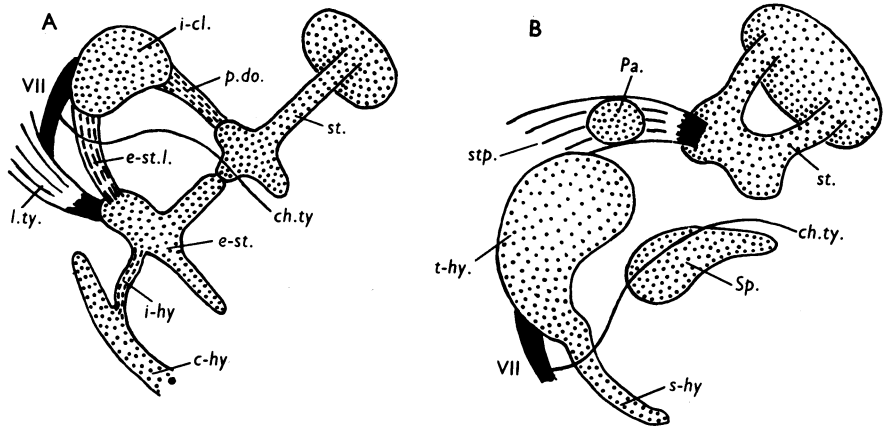


Fig. 8. Diagrams illustrating dorsal hyoid derivatives related to the right ear in a lizard (A) and a mammal (B). Whether the cartilages of Paauw and Spence can be equated to structures shown in (A) is uncertain.

of *Lacerta* a loop from the dorsal (epihyal) end of the hyoid blastema is raised up from the horizontal or hyostapedial portion and gains attachment to the crista parotica of the auditory capsule. The apex of this loop enlarges to form the intercalary cartilage between the quadrate and the squamosal; the outer or 'laterohyal' limb of the loop becomes the extrastapedial ligament joining the processus inferior or tympanic process of the extrastapes to the intercalary, and the inner limb persists for a while as the processus dorsalis or suprastapedial process and then regresses (Fig. 8A). These epihyal derivatives become separated from the ceratohyal as a result of degeneration of the intervening interhyal element. *Sphenodon* differs from the lacertid condition in that the interhyal and both limbs of the hyoid loop chondrify (see Versluys, 1904; Wyeth, 1924). The chorda tympani in lizards, in spite of Brock's statement and figure to the contrary (1932), hooks round both the processus dorsalis and the extrastapedial ligament. In mammals the hyoid cartilage makes contact with the crista parotica through the tympanohyal (Fig. 8B).

Goodrich (1916, 1930), following Versluys, homologized the mammalian tympanohyal with the reptilian intercalary. His figures indicate the processus dorsalis, hyostapes and interhyal as forming a connexion between the intercalary and the ceratohyal corresponding to the mammalian stylohyal. If this were so, there might be a case for interpreting Spence's cartilage, on account of its close relation to the chorda tympani, as a laterohyal remnant, the homologue of the extrastapedial ligament. Goodrich, however, appears to have been unduly influenced by the failure of the laterohyal to chondrify in *Lacerta*. In synapsids little is known of the fate of the dorsal end of the hyoid arch, but there is no reason why it should have conformed precisely to the commonest lacertilian pattern. According to Parrington (1955), the processus dorsalis of synapsids was probably still attached to the stapes, and may have helped in its support. As, in the ancestors of mammals, the stapes decreased in size, the processus dorsalis would no longer have been required as a supporting structure, and may consequently have undergone reduction. On the other hand, the lateral limb of the original hyoid loop may have become chondrified, forming a stylohyal for the attachment of tongue and throat muscles. On this view, part at least of the mammalian stylohyal or styloid process corresponds to the extrastapedial ligament (and interhyal) of typical lizards. The tympanohyal is the equivalent of the intercalary: in forming the medial wall of the fossa incudis (Fig. 6) it occupies a position comparable to that of the intercalary in lizards medial to the posterior flange of the quadrate (Fig. 4A). The blastema of Spence's cartilage appears to develop in the interval between the tympanohyal and the stapes, and may therefore possibly represent a processus dorsalis. It is interesting that in a newborn mouse, where no cartilage of Spence is formed, the dorsal tip of the tympanohyal, which in mice is characteristically recurved forwards, was found to be connected to the stapes by a distinct ligamentous strand running medial to the chorda tympani (Fig. 7B). This strand is not in the position of a hyostapes, but could be interpreted as a vestigial processus dorsalis.

The only link between Paauw's cartilage of mammals and the reptilian extrastapes is provided by the stapedius muscle, in whose tendon the cartilage forms. There is some reason for equating the stapedius with the laxator tympani muscle of geckonid and agamid lizards, in spite of a changed relation to the facial nerve (Goodrich, 1930). The laxator tympani is inserted into the back of the tympanic process of the extrastapes. If Paauw's cartilage is indeed a vestigial structure, it would seem reasonable, following van der Klaauw (1923) and Olson (1944), to regard it as the homologue of the extrastapedial process as a whole, forming with the tendon of insertion of stapedius a reduced version of the original cartilaginous connexion between the stapes and the tympanic membrane (Fig. 8A).

DISCUSSION

It is concluded that the tubotympanic recess of mammals is formed in the position of a submandibular diverticulum of the pharynx present as a respiratory device in modern reptiles and probably, in view of Sushkin's observations, also possessed by ancestral synapsids. The pars tensa of the mammalian tympanic membrane is an enlarged version of the reptilian drum, which has acquired a submandibular extension and become embraced by the angulare. The pars flaccida or Shrapnell's membrane

is a new upgrowth, above the original site of the upper end of the quadrate, towards the squamosal. It may get an attachment to the ectotympanic when that bone becomes completely annular. An attempt has been made to show how the reptilian type of middle ear could have been transformed without any 'saltations' into its mammalian successor during the stages of evolution following the release of the reflected lamina of the angulare and the retro-articular process of the articulare from muscle attachments.

The theory is claimed to be preferable in certain important respects to those which have been put forward previously. First of all, it fits the facts of morphology. The Eustachian tube bears the correct relation to the tensor tympani—ventral to the muscle in mammals. It accounts for the obliquity of the mammalian external auditory meatus and Eustachian tube, the former inclining downwards and forwards, and the latter upwards and backwards, towards the eardrum. At the same time, a reason is offered for the changed relation of the internal carotid and the fenestra rotunda to the tympanic cavity. The position of the chorda tympani between the pars tensa and Shrapnell's membrane is explained. The course of this nerve is not absolutely constant throughout vertebrate history. In lizards it may pierce or pass above the adductor mandibulae internus, and Gray (1958) has emphasized its variable relation in mammals to the tendon of the tensor tympani. In geckonid and pygopodid lizards there is no processus dorsalis, and the chorda tympani runs directly forward in front of the middle ear. McClain (1939) has described how in early embryos of *Didelphys* the nerve is pulled through the blastema of the stylohyal from lateral to medial. Nevertheless, other things being equal, it is an advantage not to have to postulate a shift across the tympanic membrane during the evolution of mammal-like reptiles.

Secondly, some of the obscurities in the palaeontological story are clarified. The dilemma due to the later cynodonts possessing an angulare with, apparently, ectotympanic characters, when a tympanic membrane attached to it could have had little or no auditory function, is resolved without introducing the extra hypothesis of a 'resonator' derived from the middle ear. There is no need to devise a complicated extrastapedial process which would reach to the notch of the angulare in early forms, nor to suppose that late forms redeveloped a lost tympanic membrane. If the ancestors of mammals did at one stage lose their capacity to hear by air conduction, yet possessed a submandibular sulcus, it would have been possible for them to reform a tympanic cavity entirely from it. If, as appears more likely, however, the original tympanic cavity was retained, and the mammalian middle ear chamber had a twofold origin in the manner suggested, the presence of a submandibular sulcus makes it a little easier to understand how the angulare, articulare and quadrate came to free themselves from the jaws and be taken up into the middle ear.

Thirdly, the theory is in keeping with what can be inferred from embryology; if it is true, there is in the developmental history of the middle ear in mammals a fair degree of recapitulation. The relation between the tubotympanic recess and the ectotympanic in the embryo insectivore *Potamogale* (Fig. 3B) is the same as that which it has been supposed the submandibular sulcus bore to the angulare in cynodonts. This does not necessarily mean that cynodonts were ancestral to mammals, but simply that in the angulare, as in other features, they exhibit an

intermediate condition which may also have occurred in actual mammalian ancestors. The subsequent steps which have been postulated in the theory are reflected in the ontogeny of the mammalian drum, as it appears in Insectivora such as *Elephantulus*. The external auditory meatus grows down from above the manubrium mallei to meet the tubotympanic recess above the lower arm of the ectotympanic (Fig. 5A): this corresponds to the suggested migration of the meatus in the final stages of therapsid history to meet the submandibular sulcus above the reflected lamina of the angulare. The developing tympanic membrane is at first unattached at its upper margin; the external auditory meatus meets the squamosal, and the tubotympanic recess invades the attic region so late as to lend support to the view that Shrapnell's membrane was phylogenetically a late acquirement.

Assuming it to be true that the lacertilian pharynx and middle ear retains many ancestral reptilian features, and that mammals have evolved away from the primitive pattern in the manner described, it becomes possible to compare equivalent regions of the ear in lizards and primitive eutherian mammals such as the Insectivora. Towards the back of the ear, a transverse section through the fenestra ovalis in *Elephantulus* is retropharyngeal and passes through the point of entry of the internal carotid and the cranial sympathetic trunk into the auditory capsule (Fig. 5B). A comparable section in a lizard, passing through the Eustachian tube, illustrates how the cochlea has usurped the place of the latter in mammals (Fig. 2). Anteriorly, the mammalian Eustachian tube connecting with the pharynx at the level of the alisphenoid (Fig. 3B) has obvious affinities with the lacertilian submandibular sulcus at the comparable level of the basipterygoid process and the epipterygoid (Fig. 3A). Here, too, the mammalian goniale—that is, the membranous ossification forming the long anterior process of the malleus—can be seen to bear just the same relation as the reptilian pre-articulare to Meckel's cartilage and the chorda tympani. In spite of the doubts expressed by Olson (1944) and Westoll (1944), Gaupp's original claim (1911a) seems justified that these bones are homologous. It is true that in Insectivora the goniale may be partly fused with the ectotympanic: but the two elements are quite distinct for the greater part of their extent, and a much more intimate fusion occurs between the pre-articulare and angulare amongst lizards in the Geckonidae.

The significance of the cartilages of Paauw and Spence—whether they are to be regarded as extrastapedial and suprastapedial vestiges or as mammalian neomorphs developed in response to some functional need—depends in part on whether the tympanic membrane of mammals is considered to have evolved anew or from a reptilian precursor. It is less likely that any cartilaginous appendages of the reptilian stapes would have persisted if the eardrum had once been lost. This point may never be settled beyond question, but the balance of evidence is on the whole against the view that the tympanic membrane ever disappeared entirely in ancestral premammals, even though it may have been lacking in some Synapsida. Many of the best-known and best-preserved fossils are large forms, probably off the direct mammalian line. Moreover, we know from the anatomy of lizards that, in one reptilian group at least, it is possible even within the same family for the middle ear and drum to be lost in some genera and retained in others. The embryological appearances are certainly consistent with the tympanic cavity of mammals having

been developed entirely from the submandibular sulcus. On the other hand, the mammalian middle ear could, as has been shown, have arisen as a result of the original tympanic cavity becoming merged with the submandibular sulcus, without loss of the drum. The latter alternative avoids the need to invoke parallelism to account for a structure such as the mammalian stapedius, which resembles fairly closely its reptilian counterparts in crocodiles and lizards, and which would have been unlikely to survive total regression of the tympanic membrane.

The view expressed here, that the Eustachian tubes of mammals and reptiles are not strictly equivalent, has also formed part of an evolutionary theory of the middle ear developed by Tumarkin (1955, latest statement). No support, however, can be given to his basic tenet that absence of the middle ear is invariably a primitive character, and that this organ has been and is being evolved separately by all tetrapods which possess one. Tumarkin's conclusions have been severely criticized by Parrington (1949), and Vaughn (1955) has pointed out that the concept of ear reduction is unavoidable unless hypotheses are to be multiplied beyond all the evidence. Although it is often difficult to distinguish simplicity of structure which is truly primitive from that which is regressive, an almost indisputable example of the latter is provided by the ear of the little-known lizard *Aprasia*. This small, burrowing pygopodid, unlike other members of its family, lacks a tympanic membrane and Eustachian tube. Further, there is no stapes. In the place of the footplate of the stapes, the fenestra vestibuli supports a membrane which, since the fenestra rotunda is closed, probably functions as a secondary tympanic membrane during bone-conduction of sound via the quadrate. Absence of the stapes in an adult lizard can hardly be interpreted except in terms of degeneracy.

SUMMARY

1. Objections are raised to the theory that the middle ear cavity of mammals was evolved from a diverticulum of the original reptilian tympanic cavity and that Shrapnell's membrane is a relic of the reptilian eardrum.
2. A lateral diverticulum of the floor of the pharynx is described in lizards and named the submandibular sulcus. It is claimed that this diverticulum may have been present in Synapsida and have played a part in respiration.
3. The submandibular sulcus is shown to possess relations to lower jaw structures comparable to those of the tubotympanic recess in mammalian embryos.
4. It is suggested, therefore, that the middle ear cavity of mammals may have evolved either from the submandibular sulcus alone or, more probably, by incorporation of the original tympanic cavity into the submandibular sulcus.
5. Accepting the latter alternative, the pars tensa of the tympanic membrane of mammals is regarded as an extension of the original reptilian drum, and Shrapnell's membrane as a new formation consequent upon the retreat of the bodies of the malleus and incus into the middle ear.
6. The cartilages of Paauw and Spence are interpreted as being either mammalian neomorphs or, possibly, vestiges of respectively the extrastapedial and supra-stapedial process.
7. The tympanohyal and stylohyal of mammals are probably homologous with the intercalary, together with a laterohyal element of the dorsal end of the hyoid

arch skeleton forming the extrastapedial ligament in typical lizards, rather than with the processus dorsalis and hyostapedial portion of the extrastapes.

8. A condition of the auditory capsule is described in the lizard *Aprasia*, which appears to prove that absence of the middle ear, in this tetrapod at least, is a regressive rather than a primitive character.

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REFERENCES

- BROCK, G. T. (1932). Some developmental stages in the skulls of the geckos, *Lygodactylus capensis* and *Pachydactylus maculosa*, and their bearing on certain important problems in lacertilian craniology. *S. Afr. J. med. Sci.* **29**, 508-532.
- DRUMMOND, F. H. (1946). Pharyngo-oesophageal respiration in the lizard, *Trachysaurus rugosus*. *Proc. zool. Soc. Lond.* **116**, 225-228.
- FINDLAY, G. H. (1943). The development of the auditory ossicles in the elephant shrew, the tenrec and the golden mole. *Proc. zool. Soc. Lond.* **114**, 91-99.
- GAUPP, E. (1911*a*). Beiträge zur Kenntnis des Unterkiefers der Wirbeltiere. I. Der Processus anterior (Folii) des Hammers der Säuger und das Goniale der Nichtsäuger. *Anat. Anz.* **39**, 97-135.
- GAUPP, E. (1911*b*). Beiträge zur Kenntnis des Unterkiefers der Wirbeltiere. II. Die Zusammensetzung des Unterkiefers der Quadrupeden. *Anat. Anz.* **39**, 433-473.
- GAUPP, E. (1913). Die Reichertsche Theorie. *Arch. Anat. Physiol., Lpz.*, Suppl. Bd. (1912), pp. 1-416.
- GOODRICH, E. S. (1916). The chorda tympani and middle ear in reptiles, birds and mammals. *Quart. J. micr. Sci.* **61**, 137-160.
- GOODRICH, E. S. (1930). *Studies on the Structure and Development of Vertebrates*. London: Macmillan.
- GRAY, O. (1953). The chorda tympani. *J. Laryng.* **67**, 128-138.
- GREGORY, W. K. (1951). *Evolution Emerging*. New York: Macmillan.
- KEIBEL, F. & MALL, F. P. (1912). *Manual of Human Embryology*, 2. Philadelphia and London: J. P. Lippincott.
- VAN DER KLAUW, C. J. (1923). Die Skelettstückchen in der Sehne des Musculus stapedius und nahe dem Ursprung der Chorda tympani. *Z. ges. Anat. 1. Z. Anat. EntwGesch.* **69**, 32-83.
- MCCLAIN, J. A. (1939). The development of the auditory ossicles of the opossum (*Didelphys virginiana*). *J. Morph.* **64**, 211-265.
- OLSON, E. C. (1944). Origin of mammals based upon cranial morphology of the therapsid sub-orders. *Spec. Pap. geol. Soc. Amer.* **55**, 1-136.
- PALMER, W. R. (1913). Note on the lower jaw and ear ossicles of a foetal *Perameles*. *Anat. Anz.* **43**, 510-515.
- PARRINGTON, F. R. (1934). On the cynodont genus *Galesaurus*, with a note on the functional significance of the changes in the evolution of the theriodont skull. *Ann. Mag. nat. Hist.* (10), **13**, 38-67.
- PARRINGTON, F. R. (1946). On the cranial anatomy of cynodonts. *Proc. zool. Soc. Lond.* **116**, 181-197.
- PARRINGTON, F. R. (1949). Remarks on a theory of the evolution of the tetrapod middle ear. *J. Laryng.* **63**, 580-595.
- PARRINGTON, F. R. (1955). On the cranial anatomy of some gorgonopsids and the synapsid middle ear. *Proc. zool. Soc. Lond.* **125**, 1-40.
- PARRINGTON, F. R. & WESTOLL, T. S. (1941). On the evolution of the mammalian palate. *Phil. Trans. B*, **230**, 305-355.

- ROMER, A. S. & PRICE, L. I. (1940). Review of the Pelycosauria. *Spec. Pap. geol. Soc. Amer.* **28**, 1-538.
- SUSHKIN, P. P. (1927). On the modifications of the mandibular and hyoid arches and their relations to the brain-case in the early Tetrapoda. *Paläont. Z.* **8**, 263-321.
- TUMARKIN, A. (1955). On the evolution of the auditory conducting apparatus: a new theory based on functional considerations. *Evolution*, **9**, 221-243.
- VAUGHN, P. P. (1955). The Permian reptile *Araeoscelis* restudied. *Bull. Mus. comp. Zool.* **113**, 305-467.
- VERSLUYS, J. (1904). Entwicklung der Columella auris bei den Lacertiliern. Ein Beitrag zur Kenntniss der schalleitenden Apparate und des Zungenbeinbogens bei den Sauropsiden. *Zool. Jb. 2. Anat. Ont.* **19**, 107-188.
- WATSON, D. M. S. (1951). *Palaeontology and Modern Biology*. New Haven: Yale University Press.
- WATSON, D. M. S. (1953). The evolution of the mammalian ear. *Evolution*, **7**, 159-177.
- WESTOLL, T. S. (1943). The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. *Proc. Roy. Soc. B*, **131**, 393-414.
- WESTOLL, T. S. (1944). New light on the mammalian ear ossicles. *Nature, Lond.*, **154**, 770-771.
- WESTOLL, T. S. (1945). The mammalian middle ear. *Nature, Lond.*, **155**, 114-115.
- WYETH, F. J. (1924). The development of the auditory apparatus in *Sphenodon punctatus*; with an account of the visceral pouches, aortic arches and other accessory structures. *Phil. Trans. B*, **212**, 259-368.

EXPLANATION OF FIGURES

Probable homologies

Reptilian	Mammalian
adductor mandibulae externus	temporalis and masseter
adductor mandibulae medius	pterygoid muscles
adductor mandibulae internus	tensor tympani and tensor palati
depressor mandibulae	digastricus posterior and stylo-hyoid
laxator tympani	stapedius
angulare (reflected lamina)	ectotympanic
pre-articulare	goniale
articulare	malleus
retro-articular process	manubrium mallei
quadrate	incus
intercalary	tympanohyal
extrastapedial ligament	stylohyal (part)
pterygoid	pterygoid
epipterygoid	alisphenoid
parasphenoid	tympanic process of basisphenoid

List of abbreviations

<i>a-sp.</i>	alisphenoid	<i>e-ty.</i>	ectotympanic
<i>ad.e.</i>	adductor mandibulae externus	<i>Eu.</i>	Eustachian tube
<i>ad.i.</i>	adductor mandibulae internus	<i>f.fa.</i>	foramen faciale
<i>ad.m.</i>	adductor mandibulae medius	<i>f.ov.</i>	fenestra ovalis
<i>an.</i>	angulare	<i>f.ro.</i>	fenestra rotunda
<i>ar.</i>	articulare	<i>g-gl.</i>	genioglossus
<i>b-hy.</i>	basihyobranchial	<i>g-hy.</i>	geniohyoid
<i>b-pt.p.</i>	basipterygoid process	<i>go.</i>	goniale
<i>b-sp.</i>	basisphenoid	<i>i.ca.</i>	internal carotid artery
<i>c-br. I</i>	ceratobranchial I	<i>i-cl.</i>	intercalary
<i>c-br. II</i>	ceratobranchial II	<i>i-hy.</i>	interhyal
<i>c-hy.</i>	ceratohyal	<i>in.</i>	incus
<i>ch.ty.</i>	chorda tympani	<i>l.h.v.</i>	lateral head vein
<i>co.</i>	cochlea	<i>l.ty.</i>	laxator tympani
<i>cr.p.</i>	crista parotica	<i>la.</i>	larynx
<i>dg.</i>	digastricus posterior	<i>m.ml.</i>	manubrium mallei
<i>dp.m.</i>	depressor mandibulae	<i>m-hy.</i>	mylohyoid
<i>e.a.m.</i>	external auditory meatus	<i>ma. a. & n.</i>	mandibular artery and nerve
<i>e-pt.</i>	epipterygoid	<i>Me.</i>	Meckel's cartilage
<i>e-st.</i>	extrastapes	<i>ml.</i>	malleus
<i>e-st.l.</i>	extrastapedial ligament	<i>or.</i>	orbit

List of abbreviations

<i>ot.</i>	otic ganglion	<i>st.</i>	stapes
<i>p.au.a.</i>	posterior auricular artery	<i>st.a.</i>	stapedial artery
<i>p.do.</i>	processus dorsalis	<i>stp.</i>	stapedius
<i>p-ar.</i>	pre-articulare	<i>sy.</i>	cranial sympathetic trunk
<i>p-sp.</i>	presphenoid	<i>i.ty.</i>	tensor tympani
<i>Pa.</i>	Paauw's cartilage	<i>t-hy.</i>	tympanohyal
<i>pa-sp.</i>	parasphenoid	<i>t-ty.r.</i>	tubotympanic recess
<i>ph.</i>	pharynx	<i>te.</i>	temporalis
<i>pi.</i>	pinna	<i>tg.ty.</i>	tegmen tympani
<i>pt.</i>	pterygoid	<i>tr.</i>	trachea
<i>qu.</i>	quadrate	<i>ty.c.</i>	tympanic cavity
<i>r-ar.p.</i>	retro-articular process	<i>ty.m.</i>	tympanic membrane
<i>Re.</i>	Reichert's cartilage	<i>ty.p.</i>	tympanic process of basisphenoid
<i>s.i.</i>	subiculum infundibuli	<i>ty. IX</i>	tympanic branch of glosso- pharyngeal nerve
<i>s-an.</i>	surangulare	<i>Vg.</i>	trigeminal ganglion
<i>s-hy.</i>	stylohyal	<i>VII</i>	facial nerve
<i>sm.s.</i>	submandibular sulcus	<i>XII</i>	hypoglossal nerve
<i>Sp.</i>	Spence's cartilage		
<i>sq.</i>	squamosal		