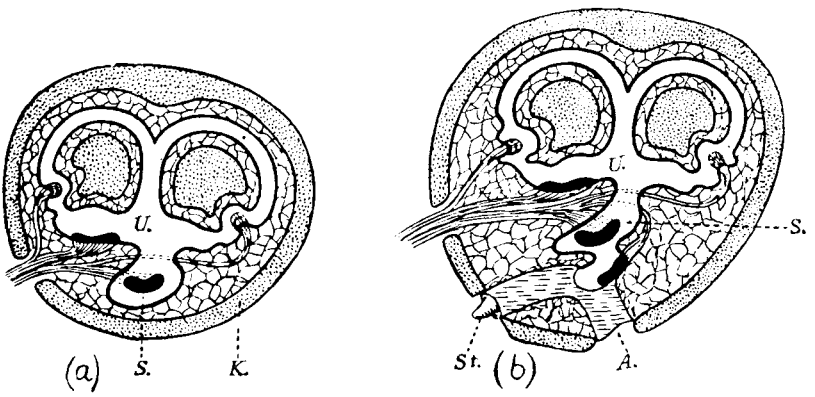
ON THE EVOLUTION OF THE AUDITORY PERILYMPHATIC SYSTEM

A. TUMARKIN (Liverpool)

THE round window may be functionally defined as the distal extremity of the perilymphatic duct, the proximal extremity being formed by the oval window. In mammals, the perilymphatic duct (consisting of the combined scalae, tympani and vestibuli) is closely applied to the scala media. So close indeed is the association that it tends to obscure the fact that ontologically and functionally the perilymphatic system is entirely different from the endolymphatic system. The latter is essentially a specialized portion of the saccule whereas the former develops as a loculation in the connective tissue surrounding the primitive labyrinth.

Fig. 1 shows the relations as envisaged by De Burlet.[1] He argues, quite correctly, that true hearing in the vertebrate does not occur except in the presence of a perilymphatic duct. The function of the duct is



FIGS. 1A AND 1B.—THE DEVELOPMENT OF THE PERILYMPHATIC DUCT.

Fig. 1A shows the primitive labyrinth completely enveloped in connective tissue. Fig. 1B shows the modifications associated with the evolution of the auditory function. At St a soft spot appears in the bony capsule. It is partly filled by a plunger. An escape port develops at A and between them the perilymphatic duct runs. Part of the neuro-epithelium of the saccule become specialized to receive the impact of the perilymphatic fluid when sound waves strike St.

S = Saccule. U = Utricle. K = Auditory capsule.

[Photograph from *Biological Reviews*, 1936, Vol. 11, p. 225.]

quite clear. It canalizes the perilymphatic fluid on to the sensitive neuro-epithelium and it should be noted that the perilymph undergoes mass movement. The distinction between acoustic energy and the energy

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of mass movement has been discussed elsewhere[2] and is of fundamental importance. It may be brought out more clearly by reference to the state of affairs found in the fish.

Fishes may be divided functionally into the ostariophysi which are characterized by the possession of a true organ of hearing and the non-ostariophysi which have no such organ. It should, not, however be deduced that the non-ostariophysi are completely insensitive to sound vibrations. Consider a fish in water in the path of a sound wave. The tissues of the animal are, functionally speaking, so similiar to the surrounding water that for all practical purposes we may assume that the sound wave passes through the fish just as it does through each lamina of water. We know that each lamina of water, when attacked by the sound wave, undergoes a phase of compression followed by a phase of rarefaction and then returns to its normal condition, the wave front having passed on. Precisely the same chain of events occurs in the fish. Every particle of the fish undergoes condensation and rarefaction. It might be thought that the bones would re-act differently from the soft tissues but actually the physical differences are not large enough to invalidate the above argument. In the skin of the fish are touch receptors which are responsive to pressure and/or deformation. *Providing the sound wave is of sufficiently low frequency, it will act as a series of touches on these receptors.* Thus the fish recognizes sound by means of its skin. This function persists in all higher animals including man, and is utilized by Gault and his School[3] for the education of deaf children. Remarkable claims have been made as to the efficiency of this vibro-tactile sense. They need not concern us here. It will suffice to note the existence of the function, which we label Mechanism No. 1.

Returning to the fish, we note that in the labyrinth, more precisely in the maculi of the saccule and utricle, specialized touch organs exist which have been seconded for the purpose of responding to gravity. They still possess the primitive sensitivity to pressure and so behave precisely as the touch receptors in the skin. In addition, however, they are provided with oto-conia and it is clear that in the process of vibration the massive oto-conia will tend to lag behind the movements of the supporting neuro-epithelium. The action will be something like that of the clapper of a bell. Thus it is that the undifferentiated saccule possesses the power of responding to sounds of low frequency. This is Mechanism No. 2. In a way the oto-conium might be regarded as a primitive type of middle ear mechanism, but leaving that aside there is no other structure in the non-ostariophysi which could be so considered. There is no perilymphatic duct and neither oval or round windows are necessary for these primitive mechanisms. The essential feature in both is that they respond to the sound wave as such. There is no conversion of the sound wave into any other form of energy.

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Evolution of the Auditory Perilymphatic System

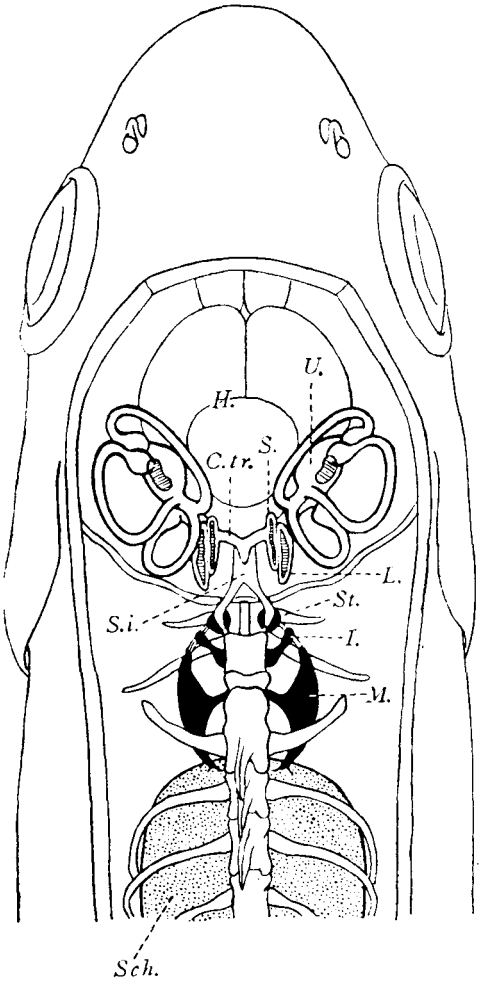


FIG. 2A.

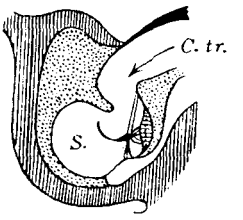


FIG. 2B.

FIG. 2A.—THE MIDDLE EAR (Weberian System) OF THE OSTARIOPHYSI.
The Weberian ossicles are black (M I and St). There is no cochlea. The saccule S (and possibly the lagena L) respond to sound waves brought to them via the perilymphatic duct Si (i.e. the sinus impar). C.tr (i.e. canalis transversalis) is part of the endolymphatic system and corresponds to the scala media of the mammalian ear.

The ossicles are analogous but not homologous with the mammalian ossicles.
The swim bladder is analogous but not homologous with the mammalian drumskin.
The sinus impar is analogous but not homologous with the scala tympani plus vestibuli.
The membranous window in the chondrocranium through which the sound waves reach S.i is analogous to the oval window of the mammal.
Note that the whole labyrinth lies free in the cranial cavity. It is not enveloped in bone.

[Photograph from *Biological Review* of Cambridge Phil. Soc., 1936, Vol. 11, p. 224.]

FIG. 2B.—THE AUDITORY END ORGAN OF THE OSTARIOPHYSI.
The whole of the saccule (except the lagena) together with its otolith has been converted into an organ of hearing. Waves in the Canalis transversus strike the specially moulded otolith and set up specific stimulation of the subjacent neuro-epithelium.

[Photograph from *Biological Review*, 1936, Vol. 11, p. 225.]

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Figs. 2A and 2B shows the auditory mechanism of the ostariophysi. Sch is a specialized portion of the front of the swim bladder. M is the tripus—a triangular ossicle derived from the transverse process of the adjacent vertebra. It has three processes. One is attached to Sch, another is attached to the vertebral column and the third passes forward to join the inter-calarium I. The latter articulates with the scaphium ST which in its turn joins the claustrum which is a small flake of bone lying in a window in the auditory capsule.

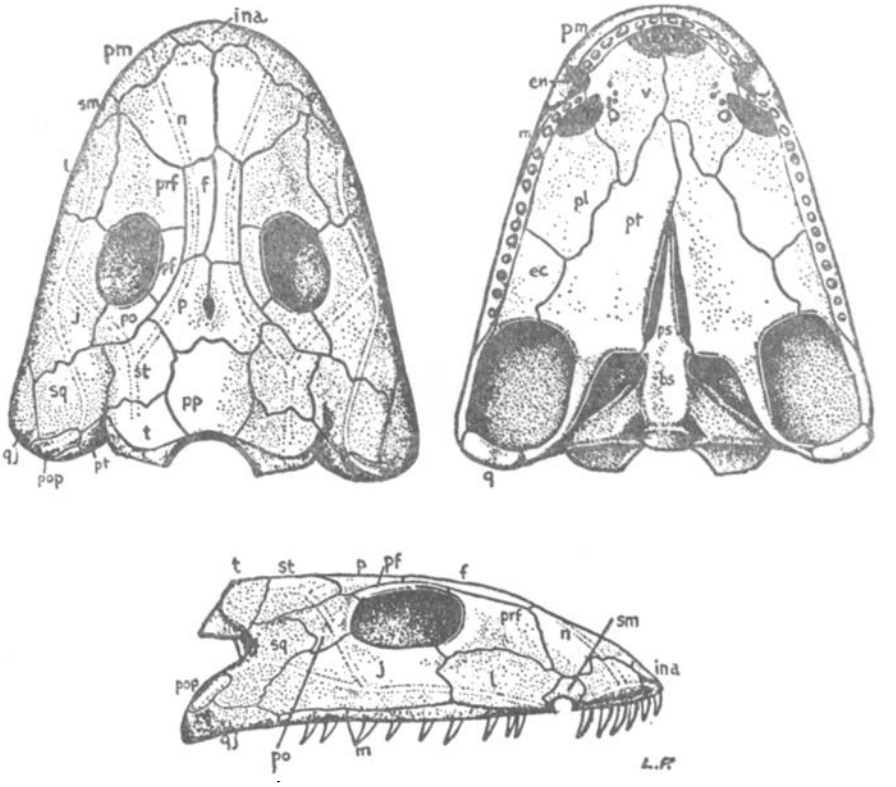


FIG. 3.—ICHTHYOSTEGA. A VERY PRIMITIVE AMPHIBIAN.

Note the distinct otic notch between tabular (t) and squamosal (sq). This animal has no oval window. Therefore it had no perilymphatic duct, and no middle ear mechanism. Its auditory function was undifferentiated i.e. Mechanisms No. 1 and No. 2. It certainly could not have had a tympanic membrane. Thus the so called otic notch has nothing to do with a tympanic membrane.

[Photograph from *Vertebrate Palaeontology*, A. S. Romer (p. 144), Univ. of Chicago Press.]

The perilymphatic duct passes forward from that point and the ducts of the two sides are joined together at the sinus impar S.i. This mechanism works as follows :

Air being very much more compressible than water, the swim bladder contracts and expands under the attack of a sound wave very much more

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violently than a corresponding volume of water would. The resulting movements of the wall of the swim bladder are further magnified by the action of the tripus which rocks en masse. These mass movements are conveyed to the perilymphatic fluid *viâ* the intervening ossicles. Mechanically this is closely comparable with the mammalian ear in which the tympanic membrane picks up the sound energy and converts it into

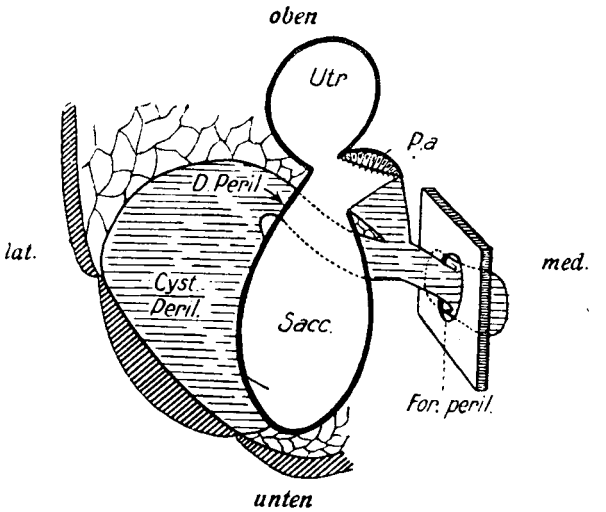


FIG. 4.—THE PERILYMPHATIC SYSTEM IN PROTEUS ANGUINEUS.

Proteus (the Olm) is a lowly urodele which inhabits the dark caves of Carniola. Its perilymphatic system is mechanically primitive. The distal end of the duct lies within the cranial cavity which it enters at the foramen perilymphaticum.
P.a.—pars amphibiorum—the portion of the saccular neuro-epithelium seconded for auditory function.

[Photograph from *Acta Otolaryng.*, 1928-9, Vol. 13, p. 159.]

mass movement in the ossicles, which in their turn set the perilymph swinging.*

The membranous area in the wall of the fish auditory capsule has a function identical with that of the oval window of the mammal. In each case, it enables the mass movements in the conducting structures external to the braincase to be transmitted to the perilymphatic duct which has developed within the brain case, and it is clear that in the absence of such an oval window the external structures could have no possible value. (Pathological closure of this soft spot, such as occurs in otosclerosis results in profound deafness.)

* This close similarity has tempted some writers to argue that the structures are homologous. That is quite incorrect. As noted above, the fish's ossicles are derived from the transverse process of vertebrae, whilst mammalian ossicles have a quite different origin.

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The auditory conducting mechanism can thus be sub-divided into three distinct units as follows :

1. The receiving component, e.g., tympanic membrane or swim bladder.

2. The transmitting chain, i.e., the ossicles.

3. The terminal component, i.e., the perilymphatic system.

The mechanism of the fish and the mammal are by no means the only ones found in nature. I have elsewhere[4] described the following six mechanisms :

(a) Vestibulo-squamosal (found in Urodeles).
(b) Vestibulo-quadrate (found in snakes and some lizards).
(c) Vestibulo-scapular (found in Anura).
(d) Vestibulo-hyoid (found in some lizards).
(e) Vestibulo-tympanic (found in many reptiles and birds).
(f) Vestibulo-ossicular (found in mammals).

These six mechanisms differ very much in respect to the receiving and transmitting components but they are all alike in possessing an oval window and a perilymphatic duct. However crude and inefficient the collecting and transmitting mechanism may be a perilymphatic duct, and oval window are always present. The reason for this is quite obvious. Hearing, so far as the vertebrates are concerned depends on the specialization of a portion of the neuro-epithelium of the saccule. This is stimulated by *mass movement* of the perilymph, i.e., Mechanism No. 3.

In the absence of an oval window the vibrations of the tympanic membrane (or swim bladder) would not reach the perilymphatic duct. This would encounter and be dissipated by the whole mass of the chondrocranium. This is literally what happens in classical otosclerosis. It follows therefore that until the oval window developed, the other elements of the auditory conducting mechanism can only have existed—if at all—in a most rudimentary form. In particular—the tympanic membrane which is characteristic of the most exquisitely perfect and recently evolved mechanism—could not possibly have existed before the oval window. Comparative anatomy provides us with many examples of primitive mechanisms—primitive that is to say as regards the receiving and transmitting elements—but in every case the oval window and perilymphatic duct are present. Thus on the basis of both morphological and physical evidence we declare that any animal which does not possess an oval window cannot have hearing of the type of Mechanism No. 3. This dictum is of particular importance in considering the hearing in primitive amphibia.

Fig. 3 shows the skull of Ichthyostega, a very primitive amphibian. The notch between the tabular and the squamosal is called the otic

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notch because it is believed that a tympanic membrane was situated thereat. But Ichthyostega does not possess an oval window. Therefore it could not have possessed a perilymphatic duct and a fortiori it could not have possessed a tympanic membrane. The otic notch—whatever its purpose—certainly did not house a tympanic membrane.

It remains now to consider the round window. Figs. 4, 5 and 6 show the perilymphatic duct in a series of animals. We have defined the round window as the distal extremity of the perilymphatic duct and on the basis of this definition it appears that in Proteus it lies within the cranial cavity. This in fact is a very common finding in animals such as Proteus which possess very primitive hearing.

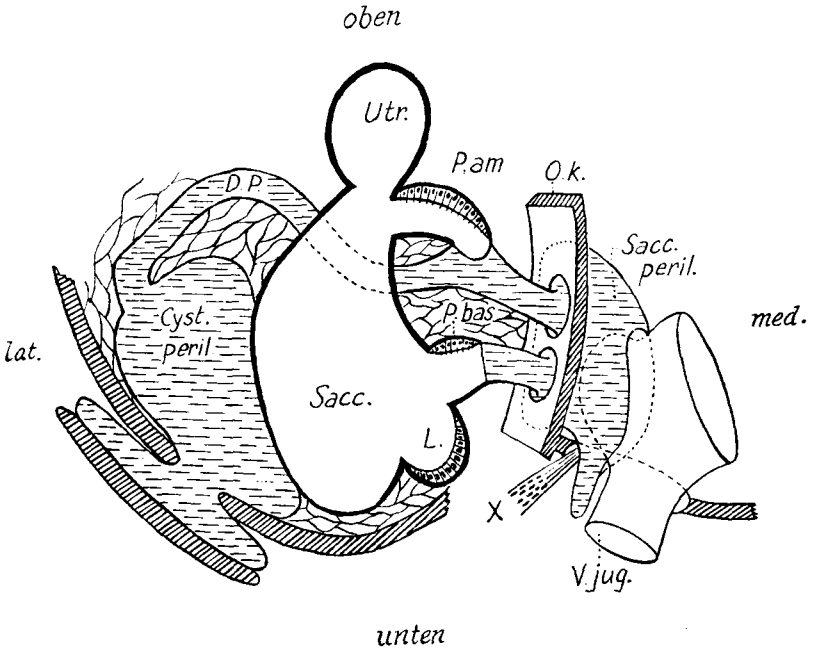


FIG. 5.—THE PERILYMPHATIC SYSTEM OF THE FROG.

Note that, in addition to the Lagena (of unknown function) the frog possesses two plaques of auditory neuro-epithelium, i.e. P.am—Pars amphibiorum and P.bas—Pars basilaris. The two ducts unite inside the cranial cavity to form the saccus perilymphaticus which then escapes via the jugular foramen.

[Photograph from *Acta Otolaryng.*, 1928-9, Vol. 13, p. 165.]

The diagrams have in fact been arranged in ascending order of efficiency and it is apparent that increasing efficiency is associated with a migration of the round window from this primitive situation inside the cranial cavity to an intermediate situation on the jugular notch and finally on to the tubo-tympanic cleft. The latter situation is only found in animals which possess a perfect tympanic membrane. The significance

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of this migration of the round window is obvious. The efficiency of any auditory conducting mechanism is closely related to the lightness and mobility of the perilymphatic system. In Fig. 4 the thrust of the stapes drives the perilymph against the counter resistance of the adjoining cerebrospinal fluid. In Fig. 6 the round window has emerged into air and the thrust of the perilymph only encounters the impedance of the air in the tubo-tympanic cleft. It thus appears that the evolution of the auditory conducting mechanism has been accompanied by a process of improvement both in the peripheral and in the central components. I have elsewhere shown that primitive animals possessed various types of crude receiving and transmitting components and that a long and tortuous process of development was necessary before the perfected

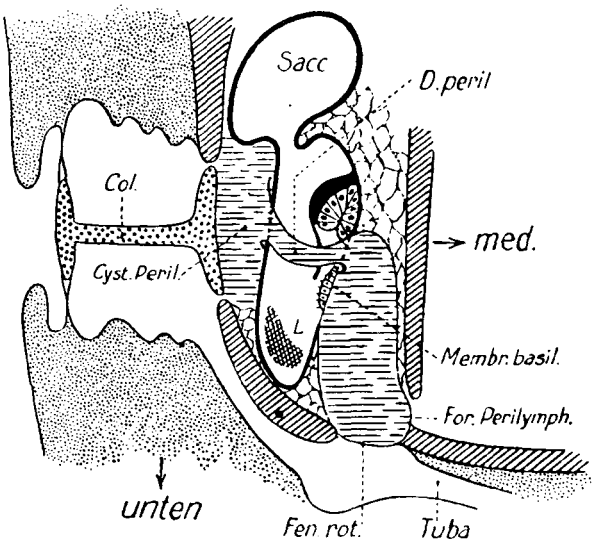


FIG. 6.—THE PERILYMPHATIC SYSTEM IN HEMIDACTYLUS (A Lizard).

Note how the ductus perilymphaticus still communicates with the cranial cavity at the foramen perilymphaticum but the main escape port is the Fenestra rotunda, opening on to the tubo-tympanic cleft.

This is—mechanically—the most efficient middle-ear mechanism with an air-borne membrane at each end, i.e. Tympanic membrane and membrane of round window.

[Photograph from *Acta Otolaryng.*, 1928-9, Vol. 13, p. 174.]

tympanic membrane with its exquisitely balanced ossicles finally emerged. It now appears from this present discussion that a comparable process was occurring at the other extremity of the conducting chain and that the hall mark of real perfection is the simultaneous possession of air-borne membranes at both extremities. i.e., Tympanic membrane proper and the secondary tympanic membrane in the round window.

It should be noted that this argument is based on the tacit assumption

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that the auditory mechanisms found in lower animals today represent stages in the evolution of the middle ear. Reasons for this belief have been deployed elsewhere. Be that as it may, the evidence of palæontology, so far as it is available, does conform to the present argument. Fig. 7 for instance, shows reconstructed casts of the inner ears of certain Therapsids. The oval window is easily recognized and so are the semi-

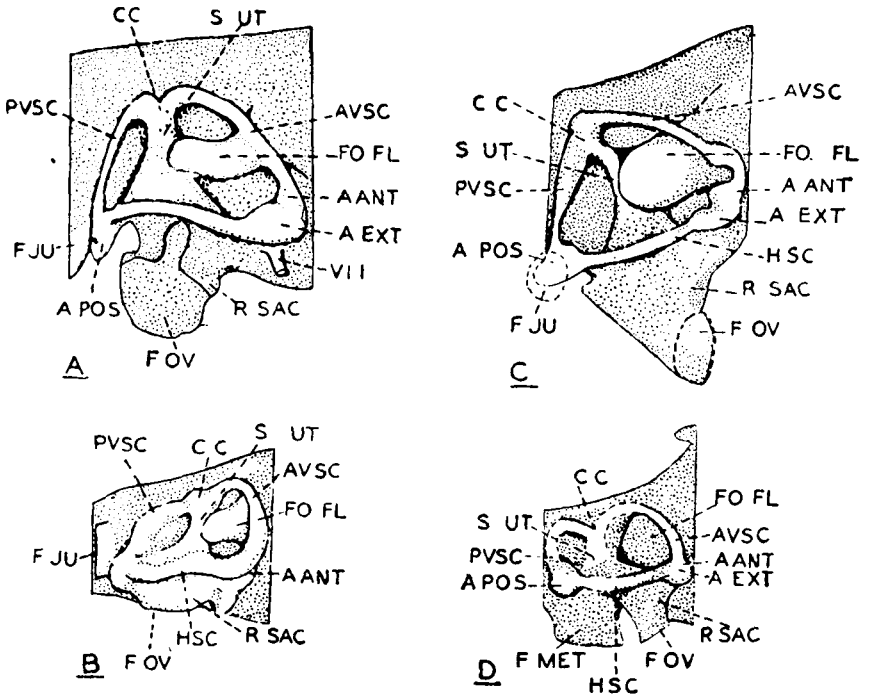


FIG. 7.—RECONSTRUCTED CASTS OF LABYRINTHS OF CERTAIN PRE-MAMMALIAN REPTILES. LATERAL VIEWS OF CASTS OF LABYRINTHS OF GORGONOPSIANS A AND B, THEROCEPHALIAN B, AND CYNODONT B.

Drawn from wax models which were reconstructed from sections. Not to scale.
A.—Gorgonopsian B, *Cistecephalus* zone. C.—Therocephalian B, *Tapinocephalus* zone.
B.—Gorgonopsian A, *Endothiodon* zone. D.—Cynodont B, horizon uncertain.
The three canals (HSC, PVSC, and AVSC) show up well with their ampullae (AANT, APOS, and AEXT).

The Fenestra ovale (FOV) opens on to the recess for the saccule (RSAC).
The Jugular foramen FJU is shown but there is no evidence of a round window.
The perilymphatic duct must have ended in the cranial cavity as in Proteus or on the jugular foreman as in the frog.

[Photograph from Special Papers Geol. Soc. of America, 1944, No. 55, p. 27.]

circular canals and the general cavity of the vestibule but there is no evidence of a round window opening externally. The presence of an oval window indicates that these animals did possess a perilymphatic duct, but the distal extremity of that duct, i.e., the round window

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opened on to the cranial cavity or possibly the jugular notch, just as it does in primitive animals today.

To sum up :

Primitive animals (whether extinct or modern) share with more highly developed animals, the ability to detect sound waves. The detector mechanisms are located either in the skin (Mechanism No. 1) or in the undifferentiated labyrinth (Mechanism No. 2) and in each case the sound wave acts directly on the detector. This primitive sensitivity should not be confused with the true auditory function (Mechanism No. 3). Although physically, Mechanisms Nos. 1, 2 and 3 are quite distinct, from the evolutionary standpoint, the distinction is by no means clear cut. It cannot be doubted that during the course of evolution, there has been a *continuous* process of transition. The labyrinth itself has developed by a gradual specialization out of the primitive epiblastic layer. Embryology provides clear evidence of this transition from Mechanism No. 1 to Mechanism No. 2.

Similarly, the transition from Mechanism No. 2 to Mechanism No. 3 must have been gradual. The oval window and perilymphatic duct did not appear overnight. Presumably the auditory capsule gradually thinned out to form the oval window whilst the perilymphatic duct with its stout fibrous wall and clear fluid content must have developed gradually as a progressive loculation in the connective tissue enveloping the primitive saccule.

True hearing (Mechanism No. 3) as the phrase is normally understood, presupposes the existence of an auditory conducting mechanism which consists of three distinct components.

1. The collecting component, e.g., drum—or swim bladder.
2. The transmitting component—the ossicles.
3. The terminal component—the perilymphatic duct.

This auditory conducting mechanism obviously cannot function in the absence of an oval window as is shown by the advanced deafness which results from ankylosis of the stapes.

The author has elsewhere described six different auditory conducting mechanisms—the differences being located mainly in the collecting and transmitting components. That is to say, Mechanism No. 3 can be subdivided into six separate groups.*

The present article deals with variations in the terminal components and draws attention to the migration of the round window which has occurred during the course of evolution. A physical explanation for that

* Further subdivision could be based on the variations in the end organ but that is a different problem. It is probable that the physical variations in the auditory end organs of different animals could be directly correlated with the variations in their auditory conducting mechanisms.

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migration is suggested—the hall mark of a perfect auditory mechanism being the existence of an air-borne membrane at both ends.

The otic notch of primeval amphibia is discussed. The theory that it housed a tympanic membrane is shown to be without foundation.

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