Mr. WATKYN-THOMAS said that in a number of cases of so-called "recurrent adenoids" one could see a felted mass of sodden mucosa extending right across the nasopharynx from one anterior pillar to the other; such a condition was frequently associated with nasal sepsis.

He did not believe that it was justifiable to leave adenoids in the presence of a chronic suppurating ear.

He had seen a true abscess cavity in an adenoid pad, and had often expressed pus from a pad.

Professor GUIDO GUIDA (in reply) said that it was the custom in Italy to test the children's hearing power before performing the operation, and sometimes before the operation the children were sent to have inhalation of calcium or iodine; for the latter a special iodine-containing water from Salso Maggiore was used. Many school children were seated in a room into which steam was introduced from a boiling kettle containing this substance and they remained for some time inhaling the vapour. The hearing of the children was tested individually, not *en masse*.

They were not usually operated upon in Italy before three years of age.

He (the speaker) used the ordinary curette, as did his colleagues.

The Swim-bladder and Weberian Ossicles and their Relation to Hearing in Fishes.

By H. MUIR EVANS, M.D.

ONE cannot do better than open this discourse with a quotation from the "Compleat Angler," by that master of prose and master-fisherman, Isaac Walton:—

"V.: But, Master, do not trouts see us by night?

"P.: Yes, and hear and smell too, both then and in the day time: and that it may be true seems to be affirmed by Sir Francis Bacon, who there proves that water may be the medium of sounds. This has made me believe that eels unbed themselves and stir at the noise of thunder. And this reason of Sir F. Bacon's has made me crave pardon of one that I laughed at, for affirming that he knew Carps that came to a certain place in a pond to be fed at the ringing of a bell or the beating of a drum; and, however, it shall be a rule for me to make as little noise as I can when I am fishing, until Sir Francis Bacon be refuted, which I shall give any man leave to do.

"All the further use I shall make of this shall be to advise anglers to be patient and forbear swearing lest they be heard and catch no fish."

We are indebted to G. H. Parker for an exhaustive critical survey of the sense of hearing in fishes (*Proc. American Phil. Soc.*, 1918). In discussing the question of "Hearing in Fishes," it is well to define what is meant by the term; for the purpose of this paper I will adopt Parker's definition and quote his words:—

"The test for hearing in fishes is the proved presence of a response mediated by the ear, and dependent upon some vibratory physical disturbance in the water, which disturbance may vary from the extreme regularity of a pure tone to the extreme irregularity of a noise, such as a report of a gun or other like explosion."

The subject can be approached from three angles: (1) From the point of comparative anatomy. (2) From a purely anatomical standpoint. (3) By the methods of experimental biology.

"Certain Teleostean families like the Siluridæ, Sciænidæ and Triglidæ seem distinguished above all others by the prevalence of some form of vocal organ" and use the air-bladder as a sound-producing organ. The Sciænidæ is a large family with about 150 species. The "maigre" or meagre (*Sciæna aquila*) is common in the Mediterranean and is sometimes taken on our coasts. It is supposed to have given rise to the legend of the sirens. H. M. Smith, in 1905, made observations on the drumming among Sciænidæ. He found that in those fish that drum the otoliths of the sacculi were exceptionally large, whereas in *Menticirrhus*, a sciænid which does not drum, they are relatively small. He came to the conclusion that the sacculus had to do with hearing and the utricle with equilibration.

Parker, in 1903, described the deep drumming sound produced by the squeteague, *Cynoscion*, which is audible when the fish is in the air at a distance of fifty feet. This sound is produced only by the males, and it results from vibrations produced by a special muscle on the abdominal organs and particularly on the swim-bladder. The females not only do not drum, but possess no special muscle. It must be allowed that unisexual sound production strongly suggests the power of hearing.

This observation and those of Smith on the otoliths of Menticirrhus therefore strongly supports the view that fish can hear. That fish can hear was the opinion of Casserius, 1610, Hunter, 1782, Cuvier, 1805, and E. H. Weber, 1830. Hunter described an experiment of a response by movement to the discharge of a gun when this was fired behind shrubs. Weber described the ossicles which bear his name and called them after the auditory ossicles of human anatomy.

It is often stated that a fish cannot hear because it has no external ear and no organ of Corti.

The first point is readily answered by a consideration of the difference in the media in which air-breathing and aquatic animals exist. Vibrations in the air require a drum for the reception of sounds, although this does not seem always necessary when one considers that in disease in which the membrana tympani is partially or completely lost, there may be very little diminution in the appreciation of sounds. In fish vibrations are received through a very different medium, and they are communicated directly through the body walls. One may, therefore, consider that the hearing in fish is analogous to what aurists call bone conduction, vibrations carried directly to the saccules through the bony walls of the fish.

It is possible that in those fish with swim-bladders and Weberian ossicles, vibrations are carried through the body walls to the air in the anterior sac, which acts as a drum, and that these vibrations are conveyed to the sacculi by means of the Weberian ossicles.

As is well known, through the work of Retzius, a typical fish has an internal ear, with a utricle, and three semicircular canals, a sacculus, with a large macula, on which rests the sagitta, and another macula in a specialized area called the lagena. This is generally held to represent that part of the internal ear which, in air-breathing animals, develops into the organ of Corti. It is interesting in this connection to compare the internal ear of the frog with that of a fish. One of the marvels of biology is the metamorphosis of the tadpole, in which the disappearance of the lateral line organs is dramatic in its suddenness and their replacement by an auditory organ is equally abrupt.

The picture of the internal ear of a frog differs very little from that of a fish. There is a ductus endolymphaticus, a utriculus with anterior, posterior and lateral semicircular canals, a sacculus with a lagena and two smaller papillæ, P. neglecta and P. basilaris.

There is nothing in the nature of an organ of Corti, and yet no one is prepared to admit that frogs do not hear. It may be interesting to give a résumé at this point of what is known of hearing in frogs.

Yerkes (1905) observed frogs in their natural habitat and found that they were stimulated by sounds:

"The sense of hearing apparently serves rather as a warning sense which modifies reactions to other simultaneous or succeeding stimuli, than as a control for definite auditory motor reactions. Experimental tests prove that sounds modify the frog's reactions to visual and tactile stimuli. When the sound accompanies the visual or tactile stimulus it reinforces the visual or tactile reaction but when given alone it never causes a motor reaction."

"Sounds modify the reaction of a frog after tympana and columella are removed. Cutting of the eighth cranial nerve causes a disappearance of the influence of sounds. It is clear then that the reactions to sounds are really auditory reactions, and that the sense of hearing in frogs is fairly well developed, although there is little evidence of such a sense in the motor reactions of the animal."

The Ostariophysi is a collective name for four families: Cyprinidæ, Siluridæ, Characinidæ and Gymnotidæ, in all of which the auditory organ has an intimate connection with the swim-bladder by means of a series of movably-connected "Weberian" ossicles of which the posterior, the tripus, is inserted into the dorsal wall of the swim-bladder ("Cambridge Natural History," vol. "Fishes"). According to Günther, out of 2,269 species of true freshwater fishes, the above four families account for 1,577 species. It is a significant fact that the Weberian mechanism is characteristic of the dominant families of the freshwater teleosts at the present day. The Cyprinidæ include the carps, roach, rudd, bream, and most of our coarse fish.

In a typical cyprinoid fish the swim-bladder is large and lies free in the abdominal cavity. It is constricted in the middle to form an anterior and posterior chamber, the latter more frequently the larger. It is joined to the œsophagus by a pneumatic duct which opens near its constricted region. The anterior end of the anterior chamber is attached to the posterior extremity of the tripus on either side:

The posterior sac of a roach is elongated and somewhat pear-shaped, with its apex projecting backwards. The base is connected with a small short duct, the ductus communicans, with the anterior sac which is roughly oval in shape and has about one-third the capacity of the posterior.

Below this duct in the posterior sac is another orifice leading into the pneumatic duct which communicates with the œsophagus. The walls of the posterior sac consist of a thin layer of involuntary muscle fibres which is reinforced by two strong lateral bands running longitudinally with a slight spiral twist from the base to the apex where they meet. These bands are continuous at their base with the fibres of a sphincter surrounding the ductus communicans. This sphincter extends downwards and is connected with another sphincter surrounding the orifice of the pneumatic duct. Exterior to the muscular coat of the posterior sac is a vascular layer; a large artery and vein pass along the line of the longitudinal muscle and divide up into smaller vessels which branch off laterally, each artery being accompanied by a vein, and finally fan-shaped arrangements of vessels extend over the whole wall and communicate with the vessels from the opposite side by a fine system of capillaries. From these capillaries a few vessels appear to pass through the muscular coat and communicate with a fine capillary network lying beneath the internal epithelial lining of the sac.

There is no red body or rete mirabile in cyprinoids, but I have observed small areas of the epithelial lining in the gudgeon showing two or three layers of epithelium, through which the small capillaries are seen to course.

The walls of the anterior sac are very differently constituted. In the first place, there is a very strong external coat, superficial to the muscular coat. It is composed of strong fibrous tissue in which the fibres have a criss-cross arrangement and are arranged in several layers. The external coat is attached anteriorly to the apex of a central bony plate which descends from the vertebral column in order to support the swim-bladder. Posteriorly it allows the ductus communicans, which is continuous with the muscular coat, to pass through a circular aperture in its coat.

If a circular cut be made near the posterior end of the external coat, the muscular coat and its contained gases can be removed *en bloc*; it will then be seen that the external coat has a slit or hiatus on its superior aspect, leaving two free edges which pass backwards and downwards from the base of the central plate. This free area is filled posteriorly with a soft tissue which seems to be similar to the membrana flaccida of the human membrana tympani. Immediately posterior to the base of the central plate will be seen on either side the posterior end of the tripus, from which, for the space of a few millimetres, fibres of the external coat spring. But from the actual tip of the tripus there springs a small muscle, which I propose to call the tensor tripodis.

This muscle is triangular in shape and is inserted by its apex into either side of a hollow, the fovea centralis, at the base of the central plate. That portion of the free margin of the external coat anterior to the tripodal attachment is attached to the tip of the central plate and runs therefore downwards in a more or less vertical direction, while the portion of the free margin posterior to the tripodal attachment runs in a longitudinal direction backwards.

It will be obvious if one looks at a specimen, how well adapted this arrangement is for the movement of the tripus, when the walls of the anterior sac are set into vibration. Where the slit or hiatus ends posteriorly, there is a central ligament which passes forwards to be attached to the vertebral column.

The attachments, therefore, of the anterior sac are firstly, to the tip of the central plate, then indirectly, by the tensor tripodis, to the base of the central plate at its lateral margins, and finally, by the central ligament, to a vertebral centrum.

The muscular coat consists of a thick sphincter which surrounds the posterior end and is continuous with the ductus communicans, and inferiorly is prolonged forwards as a broad band which bifurcates and then ends in two blind extremities, in the neighbourhood of the tripus.

The anterior sac also differs from the posterior by presenting no fan-like arrangement of capillaries or parallel branchings of arteries and veins.

The ductus communicans is not simply a duct guarded by two sphincters, one in the posterior and one in the anterior sac. It is the seat of a very complex nerve ganglion. This ganglion is supplied by the vagus, which gives off a large branch to the swim-bladder. This branch divides shortly before entering the substance of the bladder: one division ramifies round the sphincter which guards the pneumatic duct, and the other passes to the ductus communicans.

In addition to all this complex structure of what at first sight would appear to be two membranous bags filled with gas, we have to describe another complicated organ, namely, the pneumatic duct.

The pneumatic duct is a fine tube with muscular walls; as it nears the œsophagus it becomes gradually enlarged and forms what we propose to call the pneumatic bulb. Here the duct enlarges and in some fish divides up into a number of canaliculi, which finally enter an enlarged portion leading through a narrow orifice into the œsophagus.

This orifice is guarded by a strong sphincter, which is controlled by a special ganglion innervated by the vagus. In the pneumatic bulb are also a number of diverticuli which run parallel to the duct; the function of these is obscure.

An important observation has been made by Damant and myself, namely, the presence round the orifice of the pneumatic duct of a large number of taste-buds. When the fact is recalled that these fish swallow air and pump it by the pneumatic bulb into the swim-bladder, the significance of sense organs in this position is apparent.

The Weberian ossicles are four in number, named the tripus, inter-calarium, scaphoid and claustrum.

The tripus or malleus, to use Weber's original nomenclature, is crescentic in shape, with a projection in its concavity which articulates with a vertebral centrum by means of a wedge-shaped portion lying at right angles to the long diameter of the crescent. The posterior horn of the tripus is prolonged by a very fine spicule which winds round the base of the central plate, and from which arise the anterior fibres of the external coat of the anterior sac, while to its extreme tip, anteriorly, is attached the base of the pyramidal or triangular muscle, the tensor tripodis, above described.

The anterior horn of the crescent is prolonged by the inter-ossicular ligament which attaches it to a small bone, the scaphoid, and this again joins up with a circular scale-like bone, the claustrum, which forms the outer wall of the sinus impar. The interossicular ligament is supported in its centre by the inter-calarium, a small triangular ossicle the base of which rests on a vertebral centrum in front of the tripodal articulation, and is capable of executing to-and-fro movements in an oblique direction, similar to those of the tripus. The main body of the crescent of the tripus runs in a direction of about 60° upwards and forwards from the base of the central plate.

The Connection of the Ossicles with the Internal Ear. The "Cambridge Natural History" volume on "Fishes" describes this as follows :—

"The anterior ossicle (scaphium) forms the outer wall of a median backward prolongation (sinus impar) of the perilymph-containing spaces surrounding the two auditory organs. This in turn encloses a similar median prolongation (sinus endolymphaticus) from the two sub-cerebrally united endolymphatic ducts."

Bridge and Haddon made an important observation, which strongly favours the view that the Weberian ossicles are in connection with the sacculi and lagenæ. They state "there can be but little doubt that the sensory epithelium of the two saccules is solely concerned in the transmission of stimuli received through the Weberian mechanism to the eighth nerve; for the oblique valve in the ductus sacculo-utricularis must prevent the extension of any disturbance in the endolymph of the sacculi to the utricle or to the semicircular canals and their ampullæ."

The relative size of the anterior and posterior sac of the swim-bladder has an important bearing on its function. The swim-bladder is supposed to be a hydrostatic organ, and its size and extent in cyprinoids are directly correlated with this function.

Dr. Hora has pointed out that in those cyprinoid genera which live in rapidly running waters and consequently lead a ground habit of life, the bladder undergoes considerable degeneration: there is a gradual reduction of the two chambers and the posterior ultimately disappears.

The hydrostatic function of the posterior sac has been recently proved by a large series of experiments by Damant and myself. If several goldfish or roach are confined in a bell-jar full of water with a large bubble of air trapped in its top, and a current of water allowed to pass in from below and out by means of a tube at the top, and if this tube is attached to a container that can be raised to 8 or 9 feet or lowered at will, the fish without any manipulation can be subjected to the pressure they live in normally, or be subjected to a pressure of several feet of water at will.

If the pressure is raised, by raising the container, the fish at once sink to the bottom because their normal neutral buoyancy has become negative buoyancy, owing to the increased pressure acting through the compressible body-wall on the gases in the swim-bladder having produced an increase of its specific gravity. The fish almost immediately show signs of discomfort and become restless; they then start swimming upwards, and with each cessation of activity sink to the bottom; after one or two attempts they come up to the surface and suck air from the trapped bubble; they then go down again and shortly repeat the process. After a few of these excursions to the surface the container is lowered and the pressure becomes normal: it is then noticed that the fish have to swim downwards to prevent themselves from floating to the surface, and the mysterious upward lift of the fish when they cease active swimming is very striking.

A condition has been obtained of marked positive buoyancy, and this can be rendered neutral again if time is given to the fish to discharge gas from their pneumatic tube.

This experiment can be modified. If several c.c. of gas are removed from the swim-bladder of a roach and the fish is prevented from coming to the surface by a wire netting, compensation only takes place after a period of from two to four days, and in some cases much longer time is required. If the contained gases are examined in fish that have rapidly regained their neutral buoyancy by swallowing air, the analysis shows oxygen 8·9%, carbon dioxide 3·4%, whereas a normal fish has on an average oxygen 6%, carbon dioxide 2·8%. On the other hand, an analysis of the gases in a fish which has compensated without access to the surface gives oxygen 25·7%, carbon dioxide 3·4%.

Bridge and Haddon in their important monograph on the Weberian ossicles hold that the posterior sac, being larger than the anterior, acts as a sort of barometer and enables the fish through the medium of the Weberian ossicles to estimate its depth in the water. The above experiments and the comparative anatomy of the swim-bladder effectually dispel the accuracy of this supposition.

The question now arises, if the swim-bladder is primarily hydrostatic in function, what is the value to the animal, of a divided sac, with each sac controlled by a sphincter on either side of a ductus communicans in which is situated an elaborate nerve ganglion? Further, we have to inquire into the function of the chain of ossicles. It must be mentioned that the swim-bladder of cyprinoids is a high-pressure swim-bladder. A roach living normally in but a few feet of water, has an average pressure in each sac of about 60 mm. Hg or 2¾ ft. of water pressure. Experiments suggest that the pressure in the swim-bladder, if the intrinsic muscles have lost their normal tone, is somewhere about 30 mm. Hg, and that the intrinsic muscles raise the pressure normally to 60 mm., but when necessary, by their contraction, can raise the pressure to 90 mm. Hg, and even to 120 or more mm. Hg. Experiments also tend to prove that the sphincters are normally in a state of contraction, and only relax under certain conditions; they can remain closed with a positive pressure of 56 mm. Hg in one sac, while there is but a few mm. pressure in the other; in fact one sac has been laid open experimentally, while the other sac remained quite tense with a pressure of 50 mm. Hg.

Our view of the mechanism can be summarized as follows: Air gulped by the fish is directed by the taste-buds at the œsophageal orifice of the pneumatic duct into the pneumatic bulb, and is thence pumped into the posterior sac. The pressure in this sac is kept at an average of 60 mm. Hg by the intrinsic muscles; the ganglion in the ductus communicans controls the pressure in either sac, and is the special guardian of the pressure in the anterior sac; it allows relaxation of the sphincters when necessary, and governs the intrinsic muscles of both sacs. In fact the ductus communicans functions as a Eustachian tube, and controls the air pressure within the anterior sac thus allowing it to vibrate.

The vibrations of the external coat of the anterior sac are communicated to the tripus and thence by the chain of ossicles to the sinus impar and so to the sacculus, the ossicles being kept tense by the special muscle, the tensor tripodis.

Sörensen, whose views we uphold, came to the following conclusions:—

(i) The wall of the swim-bladder is capable of vibrating synchronously with rapidly recurring sound waves.

(ii) The tripus is thrown into vibrations when the wall of the bladder is vibrating.

(iii) All movements, also vibrations of the malleus, are transmitted by means of the tight interossicular ligaments to the rest of the ossicles, and in this way to the atrium sinus imparis.

(iv) The tones of the air-bladder can be transmitted to the water without losing much strength, and, if so, *vice versa*, sound waves can be transmitted from without to the air-bladder.

Hearing in Fish in the Light of Experimental Biology.—Goldfish and other fresh-water fish kept in ponds have been (it is stated) in the habit of assembling for food at the sound of a bell. Kreidl was of opinion, as the result of his experiments, that a goldfish made no response to sounds produced in air or in the water, but only reacted, as Bateson found, to the shock of a blow given to the sides or top of the aquarium. Bateson removed the auditory nerves and the attached ear sacs, and found that the fish reacted to the shocks in the same way as uninjured fish do.

Kreidl, Bateson and Lee all agreed that these observations of assembly of fish were to be explained by the sense of sight and the sense organs of the skin.

Bigelow, at Parker's suggestion, repeated Kreidl's experiments. He used as a source of sound a tuning-fork vibrating 100 times per second, and used precautions to eliminate all shocks or disturbances in the experiments. He found that fish responded to the sound by characteristic movements, and gave the same response even after one auditory nerve had been cut; if both nerves were cut the response disappeared.

Kreidl's experiments were severely criticized by Bigelow. He showed that the removal of the auditory nerve and ear sacs that Kreidl described was not in fact possible, as the sacculus and lagena cannot be removed by extracting the semicircular canals.

G. H. Parker, working with van Hensen, made some elaborate experiments. It was found that the skin was a receptor for vibrations of low frequency. When the ears were alone functional, vibrations of an order of 344 and 688 were accompanied by a response. It was also found that currents of water, and water dropped on to the surface of the aquarium, were only able to stimulate the skin.

We now come to the results described in a recent paper by F. B. Manning (1924), on the sense of hearing in goldfish. In this paper we get definite evidence of the functional use of the swim-bladder and Weberian ossicles, as experiments were devised in which only the lagena and sacculus were functional; as we have already seen, the sacculus alone receives vibrations conveyed by the Weberian ossicles from the anterior sac.

Manning experimented by means of a submerged telephone, capable of producing vibrations of from 43 to 2,752 per second on: (i) normal fish; (ii) on fish in which the utriculus was destroyed, and (iii) on fish in which the lagena and sacculus were destroyed.

He concluded that the receptor systems for sound vibrations were three in number: (1) Skin, normally up to 344 vibrations per second. (2) The lateral line system, with perhaps the same frequencies as the skin. (3) The ear consisting of the utriculus, with a range up to 688, and of a sacculus and lagena, with a range from 1,376 to an undetermined frequency above 2,752 vibrations.

The Weberian ossicles, therefore, appear to constitute an organ evolved for the detection of vibrations of a high frequency.

H. O. Bull has described experiments on conditioned responses in fishes in recent papers in the *Journal of the Marine Biological Association*, 1928-30.

The method of experimentation was the production of an associated response to food dropped into a bottle which the fish had to enter, and the vibratory stimulus of a tuning-fork or buzzer. Elaborate precautions were taken to prevent any stimuli of light, vision or noise interfering with the result. With a wrasse, conditioned responses were formed towards vibratory stimuli, using a tuning-fork of 128 d.v.'s per second, and food as an unconditioned stimulus. A conditioned response has been formed in the common eel, *Anguilla vulgaris*, towards the vibrations of an electric buzzer, using an electric shock as an unconditioned stimulus, by the same observer.

SUMMARY.

In Cyprinidæ the two-lobed swim-bladder has been shown to possess two functions. The posterior sac hydrostatic, the anterior sac a receptor for vibrations. The anterior sac has been shown by Sörensen to vibrate, and the tripus to vibrate with it.

(*a*) The sinus impar records vibrations which can only reach the sacculi.

(*b*) The series of ossicles are kept tense by a special muscle, the tensor tripodis.

(*c*) The external coat of the anterior sac has a structure similar to that of a vibrating membrane.

(*d*) The tip of the tripus is inserted in the middle of a free margin of the external coat, which is formed by a longitudinal hiatus in its superior wall.

(*e*) The posterior sac can be replenished by swallowed air. The pressure in the two sacs is controlled by the vagus acting in connection with a specialized ganglion in the ductus communicans; this latter acts as a Eustachian tube.

In the face of this cumulative evidence of an auditory function for the Weberian ossicles, we are compelled to go back to the views of Weber, and acknowledge that he had a sounder physiological vision than some of his more enlightened successors.

Discussion.—Mr. LOWNDES YATES said that in a paper, in *Science Progress*, published in 1900, Dr. Albert Gray had dealt with another aspect of this subject namely, the development of the perilymphatic sacs in carps and herrings, and had shown the extreme complexity of these sacs as they made junction with the air vesicles of the fish. Dr. Gray had pointed out that many of the further steps in man were represented in fishes.

Mr. ALEXANDER TWEEDIE said he would be glad if the lecturer could say something about innervation in connection with the swim-bladder and its relation to the eighth nerve. A Russian investigator had been making some experiments on the subject,[1] which consisted in centrifugalization and consequent destruction of the otolithic apparatus, but with the semicircular canals and muscular control of the fins left intact. Thereafter the fish were subjected to a pressure of five or six atmospheres, whilst other normal fish were placed in the same vessel as a control. The air pressure was then suddenly reduced, with the result that the normal fish at once regained their power of rising, while those which were centrifugalized remained inert.

Dr. MUIR EVANS (in reply) said he did not know the details of the innervation. At present he was working through a series of brain sections to study the comparative anatomy of the acoustico-lateral area in several members of the Cyprinidæ.

(The concluding report of this meeting will be published in the next issue of the *Proceedings*.)

1 "Bericht über die neueren russischen Arbeiten über Physiologie und Klinik des inneren Ohres," by S. Kompanejetz, *Otolaryngologia Slavica*, i, fasc. 2, 215.