THE MORPHOLOGY OF THE WEBERIAN APPARATUS OF LABEO umbratus SMITH

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ABSTRACT

In Labeo umbratus only the first three anterior vertebrae undergo any modification. These vertebrae are not completely anchylosed with each other, and are closely associated with the four Weberian ossicles. Movement is however restricted between these vertebrae since this is essential for the efficient functioning of the Weberian ossicles. The first vertebra is well developed. The absence of a spinous process and neural arch in the first vertebra may perhaps be explained by the findings of some workers who derive the claustrum from the former and the scaphium from the latter. A small muscle has its origin on the claustrum and its insertion in the angle formed by the dorsal and medial processes of the scaphium. A second muscle originates in the pit-like excavation of the first vertebra and is inserted on the ventral process of the scaphium. The intercalarium possesses horizontal, articular and ascending processes; a portion of the horizontal process being imbedded in the interossicular ligament. In Labeo umbratus it is unlikely that the intercalarium represents (if it does so at all) the entire neural arch of the second vertebra. From a morphological point of view it seems likely that the intercalarium may function as a lever. A transversely situated ductus endolymphaticus joins the two sacculi to each other. The sagitta, in the region of the ductus endolymphaticus, has a long, lateral "wing-like" process which projects into the cavity of the sacculus. The sacculus and lagena are innervated by the n. saccularis and the n. lagenaris respectively. The ductus endolymphaticus is prolonged posteriorly into a median unpaired sinus endolymphaticus. Although the only serious objection to Weber's theory is the fact that there could be no differential action of the two ears, the basic idea seems valid. Sagemehl's theory cannot be accepted. It seems likely that the Weberian ossicles are accessory structures for audition and to the hydrostatic function of the air-bladder.

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INTRODUCTION

Weber (1820) was the first to mention the connection, in the form of a row of ossicles, which exists between the air-bladder and the perilymphatic cavity of the inner ear in the families Cyprinidae, Cobitinidae and Siluridae. These ossicles lie in the saccus paravertebralis, which extends from the skull to the air-bladder. Weber (1820) regarded this chain of movably interconnected ossicles as being homologous with the auditory ossicles of mammals. These four ossicles which are aligned antero-posteriorly, Weber (1820) named in that sequence, the Claustrum, Stapes, Incus and Malleus - the latter being attached to the air-bladder.

This nomenclature of Weber is however misleading, as it was shown by later workers that the ossicles are in no way homologous with the mammalian ear ossicles, but are formed by the specialisation of portions of a few anterior vertebrae. Bridge and Haddon (1889, p. 310) therefore proposed the following nomenclature: "Instead of stapes we propose the name "scaphium", in allusion to the invariably concavo-convex or spoon shaped form of this ossicle. The "incus" may be renamed the "intercalarium", from its constant intermediate position between the "stapes" and the "malleus", when present. For "malleus" we would substitute "tripus" -- a name suggested by the three characteristic processes which this ossicle invariably possesses................ As the name "claustrum" is open to none of the objections .... it may with advantage be retained. For the ossicles collectively, including the claustrum, we would suggest the name 'Weberian Ossicles' .... instead of auditory ossicles."

Different names have been assigned to the different ossicles by various investigators. The following table [redacted] gives the nomenclature adopted by the various authors.

AUTHOR	NAME OF OSSICLES IN ANTERO-POSTERIOR SEQUENCE.			
Weber (1820)	Claustrum	Stapes	Incus	Malleus
Müller (1853)	Claustrum	Steigbügel	Ambos	Hammer
Bridge and Haddon (1889)	Claustrum	Scaphium	Intercalarium	Tripus
Thilo ('08)	Einlage	Deckel	Lenker	Hebel
Chranilov ('31)	Claustrum	Stapedoideum	Incudoideum	Malleoideum

The nomenclature to be adopted in this work, will be that of Bridge and Haddon (1889), as it does not cause any possible confusion with the non-homologous mammalian ear ossicles.
Sagemehl (1885) grouped those teleostean families possessing Weberian ossicles, under the sub-order Ostariophysi, which included the families Characinidae, Siluridae, Cyprinidae and Gymnotidae.
According to Regan ('11, p. 13 - 14) "The order Ostariophysi includes a number of types which are very divergent in form and appearance, but which agree in the possession of the remarkable Weberian mechanism forming a communication between the air-bladder and the internal ear."
The Ostariophysi (Plectospondyli) were defined by Jordan ('29) as "fishes with the anterior vertebrae modified to connect with the air bladder and inclosing an organ of hearing." He grouped the orders Eventognathi, Nematognathi, Gymnonoti and Heterognathi under the Ostariophysi.
According to Young ('55, p. 225) "The sub-order Ostariophysi is a large group of fresh water fishes, related to the Isospondyli. The anterior vertebrae are modified to form a chain of bones, the Weberian ossicles, joining the swim bladder to the ear."
Different functions have been assigned to the Weberian ossicles by different investigators. Weber (1820) was of the opinion that they were responsible for the transmission of sound waves from the air-bladder to the inner ear. This view was supported by later workers such as Sörensen (1895), Kuiper ('15), Evans ('30), Beatty ('32) and Romer ('55). Weber's theory remained undisputed for half a century, until Hasse (1872) found that this theory was unsatisfactory. He therefore propounded the theory that vibrations

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of the Weberian ossicles informed the fish of changes in the volume of the gas content of the air-bladder, which occur as a result of the different positional levels which the fish may occupy during its ascent or descent in the water. Nusbaum (1881), Bridge and Haddon (1889) and Gregory ('51) also regarded the ossicles as accessory structures for the hydrostatic function of the air-bladder. Sagemehl (1891) propounded the theory that the Weberian ossicles serve as a mechanism for the transmission of atmospheric pressure changes, which are recorded by the air-bladder and conveyed via the ossicles to the inner ear.

This investigation has been undertaken, as no work, as far as is known, has been done in South Africa on the Weberian apparatus of South African fresh water fishes. Moreover it was hoped that a study of the morphology of the Weberian apparatus might throw some further light on details of homology and function which are still disputed.

This investigation deals with the morphology of the pass auditium (Weberian ossicles) and the pars sustentaculum, the latter being a protecting and supporting unit for the former, of Labeo umbratus, a fresh water form found in the Tyumie river of the Victoria East district of the Eastern Cape Province.

MATERIAL AND TECHNIQUE

The specimens were obtained from the Tyumie river. Of the two specimens which were finally sectioned, one was fixed in Bouin and the other in formalin. Both specimens were decalcified in a solution of nitric acid and alcohol. The material was then cleared in terpineol and imbedded in paraffin wax.

Transverse serial sections of one of the specimens were cut at a uniform thickness of 20μ and of the other at 25μ. A few sections, of one of the specimens were stained with Kornhauser's quadruple stain, but this stain was abandoned because of the poor results obtained. The remaining sections were stained with Heidenhain's azan stain. The latter stain was also used in staining the sections of the second specimen.

Graphic reconstructions, as described by Pusey ('39), were made with the aid of a projection microscope. Drawings were made of the intercalarium and of the attachment of the tripus to the air-bladder and tensor tripodis ligament, with the aid of a squared micrometer fitted into an ocular of a dissection microscope.

DESCRIPTION

The length of the head of Labeo umbratus, on which this description is based, is 33.86 mm. This measurement is given so as to show the relationship, in size, between the ossicles and the head.

A. PARS AUDITUM

As already mentioned, these are four ossicles aligned antero-posteriorly on either side of the vertebral column and enclosed within the saccus paravertebralis. These ossicles form a chain between the perilymphatic cavity of the inner ear and the air-bladder. The ossicles will be described in the order in which they are arranged, beginning with the anterior ossicle and proceeding posteriorly.

1. Claustrum

The claustrum (figs. 1 and 4, CL.) extends from the posterior extremity of the basioccipital to the region of the dome-shaped portion of the scaphium, to which the interossicular ligament (fig. 1, I.L.) is attached, and lies dorsal to the anterior part of the first vertebral centrum. This ossicle, which has a total length of 0.9 mm., is composed of two parts:

(a) A ridge-like process (figs. 1 and 5, R.). This process projects dorsally and medially from the middle of the convex surface of the ossicle and extends antero-posteriorly along its entire length. [redacted] The process is imbedded in the ventral surface of a lateral cartilage (figs. 5 and 13, L.C.). The two laterally placed cartilages lie dorsal to the fibrous wall (figs. 5 and 13, F.W.) of the neural canal. Anteriorly this process attains its greatest height of 0.63 mm. which decreases to 0.21 mm. at its shortest posterior extremity.

(b) A saucer-shaped portion (fig. 5, SA.) whose concavity faces ventrally and laterally, lies lateral to the fibrous wall of the neural canal. The greatest diameter of this saucer-shaped part is 0.7 mm.

Covering the claustrum is a layer of connective tissue (fig. 5, C.T.), which is not of uniform thickness being

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much thinner on the medial than on the lateral surface. There is also a marked thickening of the connective tissue on the dorso-lateral surface where the rim of this portion is syndesmotically connected to the dorsal rim of the scaphium. The ventral rim is not attached to the scaphium.
Occupying both central portions of the above two components of the claustrum, is a cavity (fig. 5, CA.) which extends antero-posteriorly for a distance of 0.58 mm.
Attached to the posterior extremity of the ridge-like process on its ventro-medial surface, and to the surrounding connective tissue, which lies on either side of this process, is a small muscle having a length of 0.32 mm. It extends slightly medially, ventrally and posteriorly to become inserted in the angle formed by the small medial and dorsal processes of the scaphium (fig. 10, Ml.).

2. <u>Scaphium</u>

This is a thin walled saucer-shaped ossicle (figs. 1 and 5, S.) which extends further anteriorly than the claustrum. This ossicle has a length of 1.8 mm., lies lateral and ventral to the claustrum, and is composed of four parts:-

(a) <u>A saucer-shaped portion</u>. The anterior part of the concavity partly closes the apertura externa atrii (fig. 13, A.E.A.), the lateral opening of the atria sinus imparis (fig. 6, A.S.I.) —— a posterior lateral extension of the perilymphatic cavity.
At the posterior extremity of each atrium sinus imparis, a notch occurs in the lateral wall formed by the exoccipital, so that each atrial cavity is in communication with the saccus paravertebralis (figs. 6 and 13, S.P.) by way of the apertura externa atrii. The anterior portion of the scaphium which is covered on the convex surface with a fairly thick layer of connective tissue (fig. 13, C.T.) is situated 0.18 mm. posterior to the apertura externa atrii.
The ventral portion of the saucer-shaped part is syndesmotically connected along its length from the posterior portion of the basioccipital, to the anterior portion of the first vertebral centrum.

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The shape of this part, in cross section, varies from an anterior saucer-shaped appearance to a central "3"-shaped appearance (figs. 5 and 13, S.). The central portion of this "3" is the thickest paft of the ossicle. It is in this portion that a cavity appears, which extends posteriorly for a distance of 0.6 mm. Posteriorly this shape is again replaced by the saucer shape.

A dome-like outgrowth (fig. 1, D.O.) is situated ventrolaterally on the convex surfade, to which is attached the interossicular ligament (fig. 1, I.L.). It is in this dome that the cavity found in the ossicle, attains its maximum dimension.

(b) The ventral process. This process of the scaphium (fig. 1, V.P.) is situated at the posterior end of the ossicle. It is capped with cartilage and projects into a pit-like excavation on the dorsal lateral surface of the first vertebral centrum (fig. 10).

A small muscle (fig. 10, M2), which has its insertion on the ventral process and its origin in the excavation, holds this process in position. The muscle has a length of 0.4 mm.and extends dorsally, laterally and slightly posteriorly.

(c) A dorsal process. This process (fig. 1, D.P.) is dorsal to the ventral process and is attached by means of connective tissue to the fibrous wall of the neural canal. This process, which is inclined posteriorly and dorsally from the main body of the ossicle, is much longer, and extends more posteriorly, than the ventral process.

(d) A medial process (fig. 10, M.P.) which is situated on the medial surface of the scaphium, between the dorsal and ventral process. It is very short and becomes attached ventrolaterally to the fibrous wall of the neural canal. It is in the angle between this medial and dorsal processes that the muscle (fig. 10, M1.) from the claustrum is attached.

Interossicular ligament

This is a tough, relatively thick ligament (fig. 1, I.L.) in which is imbedded part of the third ossicle, the intercalarium. The interossicular ligament, which has a length of about 1.18 mm., extends posteriorly, ventrally and laterally from the dome-shaped

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portion of the scaphium, to become attached to the anterior ramus of the tripus.

3 Intercalarium

In Labeo umbratus this ossicle (fig. 1, I.), which projects posteriorly and medially, consists of:

(a) An articular process (fig. 11, AR. P.I.) which is syndesmotically connected to the dorso-lateral surface of the second vertebral centrum;

(b) An ascending process (fig. 11, ASC. P.) which is attached to the wall of the neural canal;

(c) A horizontal process (fig. 11, H. P.) which is imbedded in the interossicular ligament.

The nodular portion of the ossicle, which is imbedded in the interossicular ligament, has a length of 0.24 mm., and lies slightly posterior to the middle of the ligament.
The entire ossicle has a length of 1.78 mm. The proximal portion of the ossicle has a "fan"-shaped appearance (fig. 11). Passing between the articular and ascending processes, is the fourth spinal nerve; the ascending process lies dorsal to the ganglion of the dorsal root.

4 Tripus

This is the posterior and largest of the four ossicles, having an elongated triangular shape (fig. 1, T.), and can be divided into five parts:

(a) The anterior ramus (fig. 1, A.R.). This ramus is curved slightly medially from the anterior portion of the body of the tripus. It is to this portion of the tripus, which extends above the transverse process of the second vertebra, that the interossicular ligament is attached.

(b) The body of the ossicle (fig. 1, B.). A deep concavity which is filled with the same oily tissue as is found in the saccus paravertebralis, is found situated more-or-less in the centre of the lateral surface. On the medial surface of the body is a short ridge-like process, the distal extremity of which is highly vacuolated. This vacuolated piece of bone extends to the posterior ramus.

(c) The articular process (fig. 1, AR. P.T.). This process is long and extends dorsally and medially from the posterior

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third of the second vertebral centrum to the anterior portion of the third vertebra. This process is capped with cartilage which fits into a ventro-lateral groove in the second vertebral centrum. This groove extends from the anterior ventro-lateral to the posterior dorso-lateral surface of the second vertebral centrum. Posteriorly this process is synchondrostically attached, for a short distance, to the dorso-lateral groove.

(d) The posterior ramus (fig. 1, P.R.). As its mame implies it extends posteriorly from the body of the ossicle. This part has an elliptical shape in cross section, the central portion of which is occupied by a cavity which opens anteriorly into the concavity situated in the body of the tripus.

(e) The transformator process. The posterior portion of the posterior ramus (fig. 14) is slightly swollen at the point where it is extended posteriorly along the lateral border of the central plate (fig. 14, C.P.) as the transformator process. The latter process (fig. 14, TF. P.) curves medially to terminate more-or-less in the centre of the posterior surface of the central plate.

The "tensor tripodis muscle" (fig. 14, T.T.L.) of Evans ('25,p.559), which this investigation has shown to be a ligament, is situated on either side of the central posterior depression found in the central plate. This ligament is triangular in shape --- the apex originating on the central plate (fig. 14) and the base being inserted on the transformator process of the tripus. This ligament extends antero-ventro-laterally from its point of insertion. The tensor tripodis, though closely applied to the external coat of the air-bladder, is not part of the latter, because upon the removal of the air-bladder the tensor tripodis remains attached to the central plate.

B. PARS SUSTENTACULUM.

This comprises the first three anterior vertebrae which are associated with the Weberian ossicles. These vertebrae are not completely anchylosed with each other, but the individual members can be separated from each other with the aid of forceps. No movement is possible between individual members of these vertebrae. The first vertebra (fig. 4, V1.) is the smallest of the three and lacks a neural arch and spime. The centrum is amphicoelous,

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the anterior concavity being very shallow. The rim of the anterior concavity fits into the concavity of the basioccipital. The centrum of this vertebra is syndesmotically connected to the pharyngeal process (fig. 4, P.P.), which is a ventro-lateral projection of the basioccipital, which extends ventrally and posteriorly.

Extending laterally from either side of the centrum is a "transverse process" (fig. 1, T.P.1.) having a length of 4.07 mm. Ventral to the proximal portion of the "transverse process" is a shallow excavation, into which fits a part of the transverse process of the second vertebra.

As the neural arch is absent from the first vertebra, the wall of the neural canal is formed [redacted] by connective tissue. Dorsally this connective tissue is covered by an unpaired median cartilage (figs. 5 and 13, MED. C.) and a curved piece of cartilage (fig. 13, L.C.) which forms a "roof" over the unpaired median cartilage. Projecting ventro-laterally from either side of the median cartilage is a plate-like extension of the exoccipital (fig. 6, EXO. P.). This portion of the exoccipital lies dorsal to the notch formed in this bone, in the region of the atrium sinus imparis. From its point of attachment to the median cartilage, this plate projects ventrally, laterally and posteriorly so giving some protection to the fibrous wall of the neural canal (fig. 6). Posteriorly the dorso-lateral portions of the curved piece of cartilage (fig. 5, L.C.) ossify. The claustrum is attached to the ventral portion of this cartilage (fig. 5). The muscle (fig. 10, M2.), which is inserted on the ventral process of the scaphium, has its origin at the base of the pit-like excavation which occupies a dorso-lateral position on the centrum. The centrum of this vertebra has a number of concavities in this region.

<u>The second vertebra.</u> Both the second and third vertebrae are amphicoelous. Both transverse processes of the second vertebra curve anteriorly proximally, the curve being continued posteriorly at its distal extremity. The anterior portion of each transverse process is syndesmotically attached to an excavation in the posterior part of the first vertebral centrum.

As in the case of the "transverse processes" of the first

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vertebra, a number of excavations exists in the transverse process of the second. The anterior ramus of the tripus lies dorsal to this transverse process.

An excavation, into which fits the articular process of the tripus, is found on the centrum of the second vertebra.

The neural arch of this vertebra is only continuous with the centrum posterior to the exit of the fourth spinal nerve. A number of excavations, which are all filled with the oily tissue found in the saccus paravertebralis, are present in this region of the centrum.

The neural spine, which extends in an antero-posterior direction, is a greatly expanded plate. Anteriorly it overlies the fibrous wall of the neural canal of the first vertebra, posteriorly it partially overlies the neural arch of the third vertebra. A pair of posterior neural zygapophyses of this vertebra, articulate with the anterior neural zygapophyses of the third vertebra.

<u>The third vertebra.</u> This vertebra (figs. 1 and 4, V3.) is the largest of the three components of the pars sustentaculum. A number of excavations is present in this vertebra posterior to the attachment of the articular process of the tripus with the vertebra; the centrum here is composed of three concentric layers: an outer osseous layer, a central cartilaginous layer and an inner osseous layer.

The ossa suspensoria, "....... which is the name given to the modified ribs or ribs + parapophysis ...." (Evans '25, p. 559), are greatly expanded lateral processes of the third vertebral centrum, which curve ventrally and anteriorly, having their distal extremities expanded so forming a concavity which faces anteriorly. A number of excavations is also found in the substance of these processes.

The medial portion of each os suspensorium is expanded below the centrum into a transverse bony plate. These plates do not lie in a vertical plane but extend ventrally and anteriorly. In the centre of these two transverse bony plates is a depression, the concavity facing posteriorly. These two plates constitute the central plate, (fig. 14, C.P.).

An aperture exists in the anterior portion of the external coat of the air-bladder. The free lateral margins of the external coat, bordering the aperture, are firmly applied to a groove in the

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central plate (fig. 14). The inner coat of the air-bladder is in turn applied to the roughened posterior portion of the central plate in the region of the aperture in the external coat.
The neural spine of this vertebra is very thin and projects dorsally and posteriorly.

C SACCUS PARAVERTEBRALIS

This is a membranous bag-like structure in which the Weberian ossicles, which lie on either side of the vertebral column, are housed. The saccus paravertebralis (figs. 5,6 and 10, S.P.) of either side communicates anteriorly with the neural cavity through a lateral foramen in the exoccipitals. This foramen is situated 0.76 mm.posterior to the exit of the first spinal nerve. Posteriorly the saccus paravertebralis terminates in the region of the attachment of the transformator process to the air-bladder and tensor tripodis ligament. The connective tissue wall of the saccus paravertebralis is fairly thick. Lying within the saccus paravertebralis is an oily substance.

D NERVES ASSOCIATED WITH THE WEBERIAN APPARATUS

The first spinal nerve passes over the dorsal and lateral aspects of the posterior part of the cavum sinus imparis. A branch from the dorsal root, the dorsal ramus which supplies the skin and epaxial muscles, passes dorsally through the aperture with which the saccus paravertebralis communicates with the neural canal, to extend parallel with the supraoccipital spine. Both the dorsal and ventral roots join each other before passing out through the aperture in the exoccipital of either side.
The second spinal nerve (fig. 1, S.N2.) is given off from the spinal cord in the region of the apertura externa atrii. This nerve lacks a dorsal root. The ventral root issues from the ventral surface of the spinal cord and passes for a short distance in the connective tissue, which forms the ventral portion of the fibrous wall of the neural canal, before it passes out of the neural cavity. After leaving the neural cavity the nerve passes along the side of the ventral process of the scaphium. From the ventral process it curves anteriorly for a short distance after which it extends ventrally.
The third spinal nerve (fig. 1, S.N3.) is given off from the

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spinal cord in the region of the dorsal process of the scaphium (fig. 10). The dorsal root ganglion lies within the saccus paravertebralis, in which also the dorsal and ventral roots unite. The dorsal ramus, which supplies the epaxial muscles and the skin, is given off from the dorsal root ganglion. This spinal nerve passes between the first vertebral centrum and the nodule of the intercalarium, which is imbedded in the interossicular ligament.

The fourth spinal nerve (fig. 1, S.N4.) leaves the neural canal below the "fan"-like process of the intercalarium. The ventral root arises more anteriorly than the dorsal. The dorsal root ganglion is situated in the saccus paravertebralis where also the dorsal and ventral roots join each other. The spinal nerve curves around the medial and ventral side of the anterior ramus of the tripus to pass ventrally between the liver and the hypaxial muscle layer. This nerve also possesses a dorsal ramus which passes anteriorly and dorsally into the epaxial musculature. The neural arch and the centrum of the second vertebra coalesce with each other just posterior to the exit of this nerve.

The fifth spinal nerve (fig. 1, S.N5.) after leaving the neural canal passes over the lateral surface of the tripus. The ventral root is given off anteriorly to the dorsal root, and each root passes out of the neural canal through its own foramen in the neural arch. Part of the dorsal root ganglion lies within the saccus paravertebralis, where the dorsal and ventral roots join each other; the other part lies in the neural canal. The portion of the ganglion in the saccus paravertebralis lies dorsal to the posterior attachment of the articular process to the second vertebral centrum. Immediately after the union of the ventral and dorsal roots of this spinal nerve, a dorsal ramus is given off, which passes antero-dorsally in the epaxial musculature.

The dorsal root of the sixth spinal nerve (fig. 1, S.N6.) does not extend ventrally and posteriorly after leaving the neural arch as in the case with the former spinal nerves, but passes dorsally to leave through an opening in the neural arch situated dorsal to the opening of the ventral root. After giving off a dorsal ramus from the dorsal root ganglion, the dorsal root leaves the neural arch and passes ventrally to join with the ventral root

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opposite the exit of the ventral root. The sixth spinal nerve passes across the outer surface of the transverse process of the third vertebra.

E <u>THE INNER EAR</u>

The pars superior (Wohlfahrt, '37) is composed of the utriculus lying in, but not completely filling the utricular recess, and the three semicircular canals (fig. 2).

The pars inferior, with which this description will be mainly concerned, comprises the sacculus (fig. 2, SCC.) and lagena (LA.). The sacculus is connected to the utriculus (U.) by a short narrow duct, the ductus sacculo-utricularis (D.S.U.), in which is a valve. The anterior part of the sacculus is lodged in an excavation in the prootic, which lies ventral to the medulla oblongata.

A lamina (fig. 7, LAM.) is found in the anterior region of the sacculus and is attached to the lateral wall, so as to lie in a horizontal plane. The distal extremity of this lamina faces the macula acustica sacculi (fig. 2, M.A.S.), the sensory epithelium on which is located the sagitta (SAG.), the otolith of the sacculus. Posteriorly this lamina occupies a dorso-lateral position (fig. 7, LAM.) in the region of the ductus endolymphaticus (D.E.) where the distal extremity becomes attached to the floor of the ductus endolymphaticus so closing off the aperture between ductus endolymphaticus and sacculus.

The sacculus is innervated by the n. saccularis (fig. 3, N.S.), a branch of the auditory nerve.

The sagitta has a concavo-convex shape, in cross section, in the anterior region of the sacculus, the convexity being attached to the macula acustica sacculi. Posteriorly this otolith is composed of a central body from which radiate three "wing"-like processes, a dorsal and ventral process being attached to the sensory epithelium (fig. 7), while the third process (fig. 7, L.W.P.), which is situated between these two processes, is free and projects into the cavity of the sacculus. This process is exceptionally long where the two sacculi are joined by the ductus endolymphaticus. Posteriorly these processes disappear. The posterior portions of the sacculus and the lagena are situated in a recess formed by the exoccipital, a process of which

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overlies the lagena (fig. 7, LA.), and the basioccipital (fig. 7, BOC.) which [redacted] surrounds the ventral and lateral surfaces of the sacculus. This somewhat longitudinally placed cavity in which the pars inferior is lodged is the fovea sacculi (figs. 8 and 9, F.S.) —— sacculus and lagena almost completely filling it. The two sacculi are separated from each other by a dorso-medium projection of the basioccipital (fig. 7, BOC.). The fovea sacculi opens below the brain by a relatively large opening, one on either side. Posteriorly the fovea sacculi ends blindly, just ventral to the region where the first spinal nerve passes out through the exoccipital.

The two sacculi are joined to each other below the brain, by a transversely disposed duct, the ductus endolymphaticus. This duct is short and narrow and situated at the antero-dorsal extremity of the sacculus (fig. 2, D.E.). In this region of the ductus endolymphaticus is found the opening between the sacculus and lagena (figs. 8 and 9, AP.).

The lagena is provided with a large otolith, the asteriscus (figs. 2, 8 and 9, A.), situated on the macula acustica lagena, the sensory area of the lagena (figs. 2, 7, 8 and 9, M.A.L.). This otolith has a concavo-convex shape in cross section; the convexity situated on the sensory epithelium. The lagena is innervated by the n.lagenaris (fig. 3, N.L.), a branch of the auditory nerve.

The ductus endolymphaticus gives off a median unpaired projection which extends posteriorly. This is the sinus endolymphaticus (fig. 9, S.E.), a thin walled tube lodged in the cavum sinus imparis (C.S.I.), which it does not completely fill. The median dorsal process of the basioccipital, which separates the sacculi from each other, gives off a dorso-lateral process (fig. 9) on each side. This process meets a downward and inward projection from the horizontal expansion of the exoccipital to form the cavum sinus imparis. The sinus endolymphaticus ends posteriorly just ventral to the position where the first spinal nerve is given off. Anteriorly the sinus endolymphaticus is surrounded by reticular connective tissue, which is more concentrated dorso-laterally in this anterior region.

Posteriorly the cavum sinus imparis gives off two lateral, nearly spherical cavities, the atria sinus imparis (fig. 6, A.S.I.) which communicate with each other and with the cavum sinus imparis.

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These cavities lie on the dorsal surface of the posterior part of the basioccipital. The roof and side walls being formed by the exoccipitals --- an extension posteriorly of the bony roof of the cavum sinus imparis. Posteriorly the opening, with which the two atria communicate with each other, is closed as a result of a dorso-median projection of the basioccipital (fig. 6, BOC.), to which the exoccipitals are syndesmotically connected. Posteriorly the bony roof of the atria sinus imparis is replaced by fibrous connective tissue, which forms the floor on which the spinal cord lies. Similarly the lateral bony walls disappear leaving the atrial cavities to communicate with the saccus paravertebralis (fig. 6, S.P.). Further back this opening, the apertura externa atrii (fig. 6, A.E.A.) of Weber (1820) which is the external opening of the atrial cavities, is closed by the saucer-shaped process of the scaphium. No reticular connective tissue was observed in the atrial cavities.
Lying dorsal to the posterior portion of the medulla oblongata, and extending inwards from the junction of each exoccipital and the lateral surface of the arched supraoccipital is a membrane which forms a median unpaired cavity (fig. 12, D.C.). This cavity is enclosed dorsally by the supraoccipital. Posteriorly this horizontally placed membrane fuses with the "menix primitiva" (Weichert '51, p.602) and the connective tissue which forms the fibrous wall around the spinal cord (fig. 6), with the result that the perimeningeal space is obliterated in this region. The cavity (fig. 6, D.C.) lies anterior to the area where the first spinal nerve is given off. Posteriorly this cavity extends around the fibrous wall of the neural canal, to communicate with the apertura externa atrii where the latter is bordered by the concavity of the saucer-shaped process of the scaphium (fig. 13, OP.).

DISCUSSION

According to Sachs ('12) it is the first four anterior vertebrae in cyprinids which undergo any modification; the vertebrae posterior to the fourth are normal. Similarly Nelson ('48 and '49) working on the Weberian apparatus of Catostomidae and Rhaphiodon vulpinus respectively, found that this apparatus in each case consists of the first four anterior vertebrae and the Weberian ossicles. According to Bridge and Haddon (1889, p. 311) "...... the great majority of Siluroids agree with Amiurus in having the centrum of the second vertebra, and the centra, neural arches and spinous processes of the third and fourth vertebrae indistinguishably combined to form an apparently single vertebra, for which we venture to suggest the name of 'complex vertebra'." In Labeo umbratus it has been found that it is only in the first three anterior vertebrae that there exists any modifications. The vertebrae posterior to these are quite normal.

Sachs ('12), working on some cyprinids, found the first vertebra to be opisthocoelous. In Labeo umbratus however this vertebra is amphicoelous. The anterior concavity is very shallow when compared with the similarly placed concavities of the vertebrae posterior to this one. In this respect (i.e. its amphicoelous nature) it agrees with the finding of Nawar ('54) who worked on Clarias lazera. It differs, however, from the condition in Clarias lazera, in that the vertebra is not rudimentary, neither is it ".... situated in an elongated pit on the anterior dorsal surface of the centrum of the complex vertebra" (p. 571). Krumholz ('43) also found the first vertebra in Nematognathi to be rudimentary.

Chranilov ('26), who worked on Catostomus, found that the first vertebra carried no observable transverse processes. Bridge and Haddon (1889, p.311) state, in the case of the Siluridae, that "The first vertebra very rarely has transverse processes and even when present (some species of Arius) they are extremely rudimentary." In Labeo umbratus the "transverse processes", far from being absent or rudimentary are fairly long; in fact they are slightly longer than twice the diameter of the centrum. Sachs ('12) regards these "transverse processes" as being false, as, „Bei den Cyprinoiden ist das Ligament (which

extends/

extends from the pectoral girdle to the basioccipital in other Ostariophysi) zum Teil verknöchert, indem dessen innerstes Ende als Querfortsatz des ersten Wirbels auftritt" (p.732). Sörensen (1895) also regards the transverse processes of the first vertebra in the Cyprinidae as being false. This investigation was however unable to verify whether the transverse process of the first vertebra was false or not, as it is felt that the true nature of this process could only be determined from the ontogeny of Labec umbratus.

The absence of a spinal process and neural arch in the first vertebra may perhaps be explained by the findings of Nusbaum (1881), Wright (1884) and Matveiev ('29), who derive the claustrum from the former and the scaphium from the latter.

The first three anterior vertebrae in Labeo umbratus are not completely anchylosed with each other, as the individual members can be separated from each other with the aid of forceps. Movement is however restricted between these vertebrae. This restriction of movement may perhaps be due to the pharyngeal process which lies ventral to these vertebrae to whihh it is syndesmotically connected. This restriction of movement of the anterior vertebrae appears to be essential for the proper functioning of the Weberian ossicles, since any movement of the anterior three vertebrae, which would result from a lateral flexion of the body during locomotion, would affect the ossicles. To counteract this interference with the Weberian ossicles the pars sustentaculum must have been evolved to its present condition to ensure that no interference will affect the efficient functioning of the ossicles; and this could only have resulted from a restriction of movement of the anterior vertebrae associated with the ossicles. Bridge and Haddon (1893, p.302) state "The comparative freedom of the anterior vertebrae from anchylosis in the Cyprinidae is obviously related to the fact that the air bladder, including the anterior chamber, lies free in the abdominal cavity, and is scarcely, if at all, invested by skeletal elements; hence, as the bladder is less likely to be affected by any compression which may result from the flexure of the vertebral column during vigorous locomotor movements, anchylosis is unnecessary, or at all events does not take place to anything like the same extent as in the Siluridae." The above

statement/

statement of Bridge and Haddon (1893) that the anterior vertebrae are comparatively free from anchylosis in the Cyprinidae and that "....anchylosis is unnecessary ....", is not supported by this investigation in which it has been shown that anchylosis, though not complete, does restrict movement between the three anterior vertebrae so as to prevent any interference with the efficient functioning of the Weberian mechanism.

All four Weberian ossicles are present in Labeo umbratus. Nelson ('49, p.501) states that in Rhaphiodon vulpinus the "..... claustrum is slight to almost non-existent", and in Clarias lazera (Nawar '54) only the tripus and scaphium are present. Reissner (1859, p.431) states "....ich habe jedoch nur zwei (ossicles) gefunden ...." in Rinelepis acanthicus and in Synodontis.

Krumholz ('43 p.36) states that in Eventognathi the claustrum is "....set in the fibrous tissue of the wall of the neural canal ......". In Labeo umbratus the claustrum has no connection with the fibrous wall of the neural canal.

The claustrum is an essential unit of the apparatus, as, apart from being syndesmotically connected to the scaphium along its dorsal rim, the significance of which will be discussed when the movements of the ossicles are described, the ossicle also serves as the origin of a short muscle which is inserted on the scaphium, and as a means of protection to the fibrous wall of the neural canal.

To ascertain whether any movement of the claustrum occurs when the other ossicles are set in motion, the following experiment was performed. The Weberian ossicles and air-bladder were fully exposed, and the pneumatic duct ligatured in a recently killed specimen of Labeo umbratus. The specimen, after being pinned down laterally on a slab of wax which was firmly attached to the top of a table, was observed under a dissection microscope and pressure applied with the thumb and index fingers to the anterior chamber of the air-bladder. The tripus, intercalarium and scaphium reacted to this stimulus by moving forwards, but no movement of the claustrum was observed. Movement of the ossicle would be impossible since the stimulus (of whatever nature it may be) will not be strong enough to elicit any movement of the ossicle, as the latter is imbedded in cartilage (fig.5).

Beaudelot (1868),/

Beaudelot (1868), Grassi (1883) and Chranilov ('26) are some of the investigators who are of the opinion that the intercalarium represents the neural arch of the second vertebra. Bridge and Haddon (1893) also support the above view; they, however, go further to suggest that the intercalarium did "...... originally include an element comparable to a transverse process .... the horizontal process of the ossicle, when present, represents the modified transverse process of the second vertebra" (p.261). Sörensen (1895 p.112) however states that "a transverse process (or rib) in fishes always springs from the centrum of the vertebra, and never from the neural arch". If this is so then the view of Bridge and Haddon (1893) that the horizontal process of the intercalarium represents "the modified transverse process of the second vertebra", falls away. The horizontal process of the intercalarium cannot represent "the modified transverse of the second vertebra" as in Labeo umbratus, in which a horizontal process of the intercalarium is present, a transverse process exists on the second vertebra which projects laterally from the centrum. The horizontal process of the intercalarium is according to Sörensen (1895, p.113) an "....... ossified ligament". In Labeo umbratus it is unlikely that the intercalarium represents (if it does so at all) the entire neural arch of the second vertebra, since the arch is continuous with the centrum posterior to the exit of the fourth spinal nerve.

The interossicular ligament of Labeo umbratus is relatively thick and extends more obliquely than it does in the Siluridae. Krumholz ('43, p.36) is of the opinion that "The size and shape of the intercalarium seem to depend, to a greater or lesser degree, on the structure of the anterior ramus of the tripus. If that ramus is long and curved, ..., the intercalarium is usually small and does not articulate with the second vertebra, but if the anterior ramus of the tripus is short, as in the buffalo fishes and the carp, the intercalarium is larger and articulates directly with the body of the second vertebra." The anterior ramus in Labeo umbratus seems fairly long and yet the intercalarium is well developed. It therefore seems more likely that the size of the intercalarium depends on the length of the interossicular ligament. Where the ligament is long, the ossicle

is/

is large, as in the case of Labeo umbratus; but where the interossicular ligament is relatively short, as in the Siluridae, the ossicle does not attain the size reached in the above mentioned cyprinid. This factor of size seems again to be related to the possible function of the intercalarium. Where this ossicle is relatively large, as in Labeo umbratus, the ossicle seems, from a morphological point of view, to function as a lever, the fulcrum corresponding to the proximal portion of attachment of the ossicle to the second vertebra. Because of this attachment, the distal part of the ossicle, imbedded in the interossicular ligament, will move in a slight arc which will correspond to the direction of movement of the anterior ramus of the tripus. As a result of this action of the intercalarium, the amplitude [redacted] of the vibrations coming from the air-bladder, and transmitted from the tripus to the scaphium, will remain constant. Where the ligament is short, the anterior ramus is situated more closely to the scaphium so that the transmission of vibrations along the ligament will be quite effective without a relatively large intercalarium. This may perhaps be the explanation for the relatively small size of this ossicle in the Siluridae where the anterior ramus is situated lateral to the scaphium, resulting in a shorter interossicular ligament and a smaller intercalarium.

Bridge and Haddon (1893, p.264) are of the opinion that ".....the interossicular ligament cannot be regarded as a rigid structure, but rather as being more or less compressible .....". According to them the nature of the ligament is more like that of a muscle -- any movement of the anterior ramus of the tripus below a certain level of intensity would at first only cause a swelling or straightening of the ligament.

To ascertain whether the interossicular ligament is of a "lax" nature, as contended by Bridge and Haddon (1893), the following experiments were performed:

1. In a recently killed specimen of Labeo umbratus all the connections of the scaphium were loosened, with the exception of that of the ventral process with the centrum of the first vertebra. The attachment of the tripus was also loosened from the air-bladder and tensor tripodis ligament. After this was done it was observed that the

scaphium/

scaphium projected more laterally than in its normal position, indicating that this ossicle was pulled into this position by the ligament. The ligament could hardly have brought about this change in the position of the ossicle had it been of a "lax" nature. This experiment confirms a similar experiment done by Sörensen (1895) on Cyprinus carpio, showing that this ligament is of an elastic rather than of a "lax" nature.

2. In a recently killed specimen of Labeo umbratus the Weberian ossicles and air-bladder were exposed and the pneumatic duct ligatured. The specimen was pinned laterally on a slab of wax attached to the top of a table to ensure that no movement of the specimen should ensue upon the stimulation of the air-bladder. Observations of the movement of the Weberian ossicles were carried out with the aid of a dissection microscope which had a microscopic grid fitted into an ocular. It was possible to observe the extent of the movements of the ossicles quite well with the aid of this grid. The anterior chamber of the air-bladder was lightly pressed with the thumb and index finger. Using the grid, it was possible to deduce to what extent the ossicles were moved anteriorly and also whether the extent had been the same in the case of the scaphium, intercalarium and tripus. From these observations, undertaken with the aid of the microscopic grid, it was concluded that the three ossicles were displaced anteriorly to the same extent. This fact indicates that the intensity of the stimulation is not decreased as the stimulus is conducted anteriorly, as would be the case if the interossicular ligament was analogous to a muscle, as maintained by Bridge and Haddon (1893).

Evans ('25, p.559) working on some Cyprinidae states that "Immediately external to the central depression on either side two small triangular muscles arise. .... I propose the term tensor tripodis for this muscle". In this investigation it was found that this "muscle" of Evans is a ligament. A similar ligament was described by Nelson ('48) in the Catostomidae.

According/

According to Bridge and Haddon (1889, p.313) "The insertion of the crescentic processes of the tripodes is always into the dorsal wall of the anterior chamber of the air bladder in the normal Siluridae, or into the corresponding walls of the laterally situated air sacs in the abnormal forms ...." This description of the attachment of the transformator process of the tripus is however not very accurate for Labeo umbratus. In this case it has been shown that the attachment of the transformator process is both to the tensor tripodis ligament and to the external coat of the anterior chamber of the air-bladder.

Bridge and Haddon (1893, p.263) state that "The characteristic curvature of the crescentic process of the tripus apparently serves no other purpose than that of increasing the surface required for its connection with the fibres of the air bladder." This statement of theirs does not seem to be wholly correct. It seems more likely, as Evans ('25, p.563) states, that "....the characteristic curvature is the only way in which the tension on the tripus could be maintained, ...; and that the curvature gives the necessary leverage whereby the tensor muscle can pull in the direction (viz., downwards, outwards and forwards) required to keep tension on the series of ossicles."

Apart from bathing the inner ear, the perilymph also fills the cavum sinus imparis so that the sinus endolymphaticus comes to "float" in the cavum sinus imparis. The sinus endolymphaticus is however limited in its extent of movement in the cavum, owing to the presence of reticular connective tissue which surrounds this structure. Posteriorly the perilymph extends into the atria sinus imparis.

According to Sörensen (1895, p.417) "When the sound waves strike against the body of the fish, and the vibrations are transmitted to the air bladder, the first momentary, movement of the latter will consist in the contraction of the organ itself .....", as a result of which the tripus is pulled slightly backwards and inwards. This in turn causes the remaining ossicles to be drawn posteriorly and the saucer-shaped process of the scaphium away from the apertura externa atrii. The scaphium is pulled ventrally by the muscle which has its insertion on the ventral process of the scaphium and its origin in the pit-like excavation on the first vertebral centrum. This posterior

movement/

movement of the ossicles results in a backward flow of perilymph. At the next movement of the air-bladder, which will be in the nature of an expansion, the tripus will be moved forwards so as to cause a similar movement of the other ossicles. The tensor tripodis ligament pulls the tripus downwards, outwards and forwards. As a result of the push exerted by the scaphium, the perilymph which bathes its concavity and that of the claustrum will be moved forward. It seems as if the arrangement of the claustrum and scaphium is such that any forward movement exerted by the scaphium will cause the perilymph, which occupies the small dorsal space (fig. 5, D.S.) formed by these two ossicles, to be moved with some force through the opening which exists between the scaphium and the ventral rim of the claustrum. The perilymph of each atrial cavity will be moved forward through the common opening existing between these two cavities, and then anteriorly into the cavum sinus imparis. This forward movement of the perilymph will affect the sinus endolymphaticus which lies in this cavity. Bridge and Haddon (1893, p.267) are of the opinion that the sinus endolymphaticus " .... must be compressed .... " as a result of the flow of the perilymph. But it is possible that this structure may not undergo any compression at all. Perhaps oscillatory waves may be set up in the perilymph, as a result of the movements of the scaphia, and these waves may affect the endolymph enclosed in the sinus endolymphaticus.

It seems likely that the reticular connective tissue which surrounds the sinus endolymphaticus will affect the forward movement of the perilymph; but the extent to which it affects this is not certain.

The vibrations are conducted from the sinus endolymphaticus to the ductus endolymphaticus, and then into the sacculus of either side. As can be seen from figure 7 the lamina (LAM.) found in this part of the sacculus is situated in such a position that the vibrations, which impinge upon it, will be directed from it onto the lateral "wing"-like process of the sagitta, which attains its greatest length in this region. It is most probable that this feature will increase the efficiency of this otolith in recording the slightest vibrations transmitted to the sacculus, for if this lateral process were of a shorter length, the vibrations would have to be of a greater amplitude to

affect/

affect the otolith. Since the otolith is situated on the macula acustica sacculus, any movement of its "wing"-like process will be transmitted as an impulse from this sensory area along the n. saccularis, a branch of the auditory nerve, to the brain. As the opening between the sacculus and the utriculus is closed by a valve situated in the ductus sacculo-utricularis, no disturbance will be caused in the endolymph of the pars superior. According to von Frisch ('37 - '38, p.705) „Es wird angenommen, dass der Sacculus des Ostariophysen für die Aufnahme von Schallreizen specialisiert ist, die ihm von der Schwimmblase her auf dem Wege über die Weberschen Knöchelchen zugeleitet werden, während die Lagena durch das „Lagenafenster" in der seitlichen Schädelwand für die unmittelbare Aufnahme von Schallreizen eingerichtet erscheint."

It seems likely that the way in which the pressure, which may be too great during the inward movement of the scaphium, is counteracted, is that some perilymph flows into the cavity (fig. 6, D.C.) which lies dorsal to the spinal cord.

According tb Watson ('39, p.468) "A necessary condition for the successful reception of vibrations by the anterior part of the air-bladder .... would be that the pressure of the cotained gas should be kept at a certain uniform level." This is brought about by the nerve plexus of the vagus which surrounds the ductus communicans, and the sphincter muscle which also surrounds the ductus and which is connected with the nerve plexus. These two structures function as a mechanism for maintaining a uniform pressure in the anterior chamber.

THEORIES AS TO THE FUNCTION OF THE WEBERIAN OSSICLES

1 Weber (1820), who discovered these ossicles, assigned to them the function of transmitting sound waves from the air-bladder to the inner ear.

Objections have been raised to this theory: such a transmission of vibrations from the water to the air-bladder must be accompanied by a great loss in intensity, especially in those Ostariophyseae in which large portions of the alimentary canal surround the air-bladder; the walls of the anterior chamber of the air-bladder are unsuitable for recieving vibrations; the fish will have no cognizance as to the

direction/

direction from which the sound is coming; the contention that the interossicular ligament is "lax"; the possessors of this structure do not have exceptional powers of hearing.
Some of these objections are themselves, however, open to criticism.

Sörensen (1895) has shown that in those fish which emit sounds, the vibrations are transmitted to the water without much loss of strength, and if this is the case, then the converse will also be true i.e., that sound waves can be transmitted from the surrounding medium to the air-bladder without much loss of strength. It seems likely that the emission of sound may serve the purpose of either warning individuals of the same species against danger, or of scaring away an attacker, or for a sexual purpose. It hardly seems likely that these animals would be endowed with the ability to emit sounds, if the latter could not be heard by members of the same species. According to Sörensen (1895, p.422) "...... the fish is endowed with a sharper hearing for sounds, emitted by (the air bladder in) other specimens of the same species, so that fishes of the same species are able to hear each other at a greater distance than other sounds of the same intensity."

Evans ('25) has found that the walls of the air-bladder are quite suitable for the reception of vibrations. Sörensen (1895, p.423) states that "The wall of the air-bladder is capable of vibrating synchronously with rapidly recurring sound waves."

It has already been shown that the interossicular ligament cannot be regarded as being of a "lax" nature. Evans ('25,p.571) is of the opinion that "The tensor tripodis .... adds further evidence to this view of the state of the tension of the chain of ossicles."

But the most serious objection to Weber's theory is the fact that there could not be any differential action of the two ears, which could inform the fish from which direction the sound comes. Evans ('25, p. 571) states, "A vibration received on one side of the anterior sac would seem to be more powerful on the side received, as this band (i.e. the inferior

longitudinal/

longitudinal band of involuntary muscle of the air-bladder.) would tend to check the vibration transmitted to the opposite side." Even if this statement is true, no differential action would be possible, since the vibrations, transmitted by the ossicles to the perilymph, will affect the single median sinus endolymphaticus, from which it will be conducted to the ductus endolymphaticus and thence to the sacculus of either side, thus affecting each sacculus at the same moment and to an equal extent. Sörensen (1895, p.420) however feels that this is of no real importance, because if this was so then ".... no human being would be able to decide if a sound arises before or behind him, when the direction of the sound co-incides with the symmetrical plane of the body." Nevertheless this is an important objection to Weber's theory, and the analogy which Sörensen draws only affects man in a single plane, whereas this effect occurs in all planes as far as it concerns the fish. If the fish is able to discern the direction from which the sound comes, then the mechanism for this conception may most probably be of a nervous nature located in the walls of the sinus endolymphaticus. But this will have to be verified by selectively staining sections to ascertain whether there is any innervation of the sinus endolymphaticus. Apart from this objection the basic idea of Weber's theory seems valid.

Kuiper ('15) and von Frisch ('36) showed that the ossicles serve as a mechanism for the transmission of vibrations from the air-bladder to the inner ear. After destroying the Weberian ossicles, Kuiper ('15) noted that the fish so treated no longer reacted to vibrations, although they still reacted to other types of stimuli such as pressure changes, static disturbances... ..... etc.

The experiments of von Frisch ('37 - '38) have shown that sound vibrations, which are conducted along the chain of ossicles are received by the sacculus and lagena and that the degree of hearing in the <u>Ostariophyseae</u> is acute.

von Frisch ('38) did some experiments to test the hearing ability of <u>Amiurus nebulosus</u> in which the eyes had been removed. When ever he fed this animal, he whistled. After a few days the fish came out of its place of hiding when he whistled without presenting the food. According to him,

whistling/

whistling had acquired a biological significance. His conclusion cannot be accepted, as it is a known fact that sound waves are transmitted with very great difficulty from air to water, and vice versa, so that it is improbable that whistling sounds will be transmitted to the fish. It is more likely that the fish became donditioned and responded to vibrations set up by the tread of the approaching worker.

Evans ('25, p.563), in support of Weber's theory, states that ".... the arrangement of the ossicles seems peculiarly designed for the purpose of recording rapidly recurring movements of small amplitude."

2. Hasse (1872) was of the opinion that the Weberian ossicles served as a mechanism for informing the fish of pressure changes brought about in the gaseous content of the air-bladder during its ascent or descent in the water.

According to this author (1872, p.472) „Der sinus impar ist nach meiner Auffassung nur eine einfache, kurze, cylindrische, dünnhäutige Verbindungsröhre zwischen den Sacculi beider Seiten ...... nie habe ich den Sinus impar sich in eine, in der Cavitas gelegene Röhre fortsetzen sehen ....." As a result of this finding he came to the conclusion that the variations of pressure, conducted from the air-bladder along the Weberian ossicles, will have no effect — or very little — on the endolymph of the ductus endolymphaticus but will be manifested on the brain.

In 1873 however he revised his original opinion and concluded that the variations of pressure will be nervously recorded in the spinal cord, and not in the brain.

But from the present investigation [redacted] it seems probable that vibrations — of whatever nature — will stimulate the sagitta which will then transmit the impulse along the n. saccularis, a branch of the auditory nerve, to the brain.

Bridge and Haddon (1893) adopted this theory of Hasse, but with the following modification — that the impulse is conducted along the n. saccularis to the brain.

3. Sagemehl (1891, p.592) maintains that „Des meisten Fischen dient die Schwimmblase einfach als hydrostatischer Apparat. Bei den <u>Ostariophysen</u> erlangt sie eine neue Funktion, indem sie mit dem Weber'schen apparat in verbindung tritt und

nunmehr/

nunmehr auch als barometrischer Apparat benutzt wird."

This view is untenable as it is known that any significant variation of atmospheric pressure usually takes place very gradually, and for the fish to be able to perceive this gradual variation it must remain at the same depth for quite a time. The slightest vertical movement will affect its perception of the atmospheric pressure variations. It is hardly likely that the fish will remain stationary for any length of time. Even if this theory were correct, it is difficult to see of what importance the perception of atmospheric pressure variations would be to the fish.

Sagemehl was of the opinion that since most Ostariophyseae, especially the Siluridae, are bottom dwellers, the possession of an air-bladder serving a hydrostatic function would be of no use to its possessor. As a result of this opinion he ascribed an accessory barometric function to the Weberian ossicles. Bridge and Haddon (1893) have shown however that most of the Ostariophyseae are not bottom dwellers.

In conclusion it seems likely that the Weberian ossicles are accessory structures for audition and to the hydrostatic function of the air-bladder. To enable the fish to distinguish between the two stimuli, it is possible that there may be a slight difference in the nature of the stimuli produced by hydrostatic pressure variations, and those brought about by ordinary sound waves.

Rapidly recurring sound waves, impinging on the anterior chamber of the air-bladder will produce such movements of the ossicles which may set up oscillatory waves in the perilymph and this disturbance in the perilymph will result in a similar disturbance in the endolymph, enclosed within the sinus endolymphaticus, without there being any compression of the latter structure. As a result of this disturbance in the endolymph there will not be an actual forward flow of the endolymph towards the sacculi, but the vibrations will be transmitted along the endolymph to impinge eventually on the "wing"-like process of the sagitta. As already mentioned this otolith is situated on the macula acustica sacculi, a sensory area innervated by the n. saccularis, along which the impulse

will/

will then be conducted to the brain.

In the case of a sudden variation in pressure due to a rapid descent or ascent, the tension set up in the air-bladder will be transmitted along the Weberian ossicles to the apertura externa atrii, where the scaphium will exert a force which will be of a longer duration and of a more forceful nature than that exerted by sound waves which cause rapid movements of the scaphium thus setting up the above mentioned oscillatory waves. As a result of this force exerted by the scaphium, which results from pressure variations, there will be a forward flow of the perilymph. This in turn will result in the compression of the exceptionally thin walled sinus endolymphaticus and so causing a forward flow of the endolymph into the sacculi, from where the impulse will be conducted along the n. saccularis, to the brain. In this way the fish will be informed of any pressure changes in the surrounding milieu.

This is of course mere speculation, and experiments will have to be done to verify it.

The following suggestions are proposed for future investigations on the Weberian ossicles.

1. If there is any differential action of the ear in hearing, it seems likely that the place where this differential action will occur, will be in the sinus endolymphaticus. Selective staining of sections to indicate the innervation (if any) of the sinus endolymphaticus will therefore have to be carried out.
2. Accurate experimental investigations to determine the actual function(s) of the Weberian ossicles.
3. As there is so much controversy as to the homology of the Weberian ossicles, it would be essential for an accurate study to be made to determine the exact homology of these ossicles.

SUMMARY.

1. The Weberian apparatus consists of the three anterior vertebrae.
2. These vertebrae are not completely anchylosed with each other; movement is however restricted between them [redacted] since this is essential for the efficient functioning of the Weberian ossicles.
3. The first vertebra is amphicoelous and well developed. The absence of a spinal process and neural arch in the first vertebra may perhaps be explained by the findings of some workers who derive the claustrum from the former and the scaphium from the latter.
4. The ossa suspensoria are situated on the third vertebra.
5. All four Weberian ossicles are present.
6. A small muscle originates on the claustrum and is inserted between the angle formed by the dorsal and medial processes of the scaphium.
7. A muscle originates in the dorso-lateral pit formed in the first vertebral centrum and is inserted on the ventral process of the scaphium.
8. The intercalarium is well developed and possesses horizontal, ascending and articular processes. In Labeo umbratus however, it is unlikely that the intercalarium represents (if it does so at all) the entire neural arch of the second vertebra. From a morphological point of view it seems likely that the intercalarium may function as a lever.
9. The interossicular ligament is not "lax".
10. The tripus is attached anteriorly to the interossicular ligament and its posterior portion, the transformator process, is attached by the tensor tripodis ligament to the central plate and to the external coat of the air-bladder.
11. The apertura externa atrii communicates with the saccus paravertebralis.
12. An unpaired median thin walled sinus endolymphaticus is situated in the cavum sinus imparis. Anteriorly the sinus endolymphaticus is surrounded by reticular connective tissue.
13. A transversely situated duct, the ductus endolymphaticus joins the sacculi to each other.

14. In the region of the ductus endolymphaticus the sagitta has a long lateral "wing"-like process which seems well adapted for recording the slightest vibrations conducted along the endolymph.
15. A lamina is situated in the sacculus.
16. The sacculus is joined to the utriculus by the ductus sacculo-utricularis in which is situated a valve which prevents any distmrbance of the endolymph in the pars inferior affecting the endolymph of the pars superior.
17. The sacculus is innervated by the n. saccularis, and the lagena by the n. lagenaris, branches of the auditory nerve.
18. Although the only serious objection to Weber's theory is the fact that there could be no differemtial action of the two ears; the basic idea seems valid.
19. Sagemehl's theory cannot be accepted.
20. It seems likely that the Weberian ossicles are accessory structures for audition and to the hydrostatic function of the air-bladder.

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ABBREVIATIONS USED IN THE FIGURES.

A.	Asteriscus.
A.E.A.	Apertura externa atrii.
AP.	Opening between lagena and sacculus.
A.R.	Anterior ramus.
AR. P.I.	Articular process of intercalarium.
AR. P.T.	Articular process of tripus.
ASC. P.	Ascending process.
A.S.I.	Atria sinus imparis.
BOC.	Basioccipital.
B.T.	Body of tripus.
CA.	Cavity.
CL.	Claustrum.
C.P.	Central plate.
C.S.I.	Cavum sinus imparis.
C.T.	Connective tissue.
D.C.	Dorsal cavity.
D.E.	Ductus endolymphaticus.
D.O.	Dome-like outgrowth.
D.P.	Dorsal process.
D.S.	Dorsal space.
D.S.U.	Ductus sacculo-utricularis.
D.T.	Dorsal tendon of air-bladder.
EXO.	Exoccipital.
EXO. P.	Exoccipital plate.
EXT. C.	External coat of air-bladder.
F.S.	Fovea sacculi.
F.W.	Fibrous wall.
H.P.	Horizontal process.
IC.	Intercalarium.
INT. C.	Internal coat of air-bladder.
I.L.	Interossicular ligament.
LA.	Lagena.
LAM.	Lamina.
L.C.	Lateral cartilage.
L.EXT. C.	Lateral margin of external coat.
L.W.P.	Lateral "wing"-like process.
M.	Membrane.

M1/

M1.	Muscle.
M2.	Muscle.
M.A.L.	Macula acustica lagena.
M.A.S.	Macula acustica sacculi.
MED. C.	Median cartilage.
M.P.	Medial process.
N.L.	n. Lagenaris.
N.S.	n. Saccularis.
OP.	Opening of dorsal cavity.
O.S.	Os suspensorium.
P.P.	Pharyngeal process.
P.R.	Posterior ramus.
R.	Ridge-like process.
S.	Scaphium.
SA.	Saucer-shaped portion.
SAG.	Sagitta.
SCC.	Sacculus.
S.E.	Sinus endolymphaticus.
S. N2.-6.	Second to sixth spinal nerve.
SOC.	Supraoccipital.
S.P.	Saccus paravertebralis.
T.	Tripus.
TF. P.	Transformator process.
T.P1. -2.	First to second transverse process.
T.T.L.	Tensor tripodis ligament.
V1. -3.	First to third vertebra.
V.P.	Ventral process.

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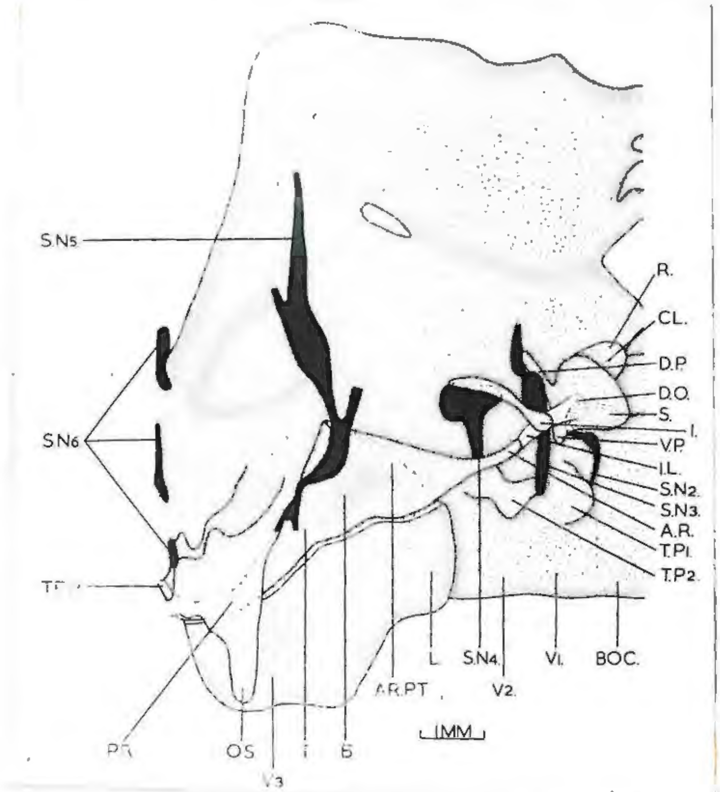

Fig. I

Graphic reconstruction of the Weberian apparatus.

Lateral view.

A.R., anterior ramus ; AR.P.T., articular process of tripus ; B., body of tripus ; BOC., basioccipital; CL., claustrum ; D.O., dome-like outgrowth ; D.P., dorsal process ; I., intercalarium; I.L., interossicular ligament ; L., liver ; O.S., os suspensorium ; P.R., posterior ramus ; R., ridge-like process ; S., scaphium; S.N2.-6., second to sixth spinal nerve ; T., tripus ; TF.P., transformator process ; T.PI.-2., first to second transverse process ; VI.-3., first to third vertebra ; V.P., ventral process.

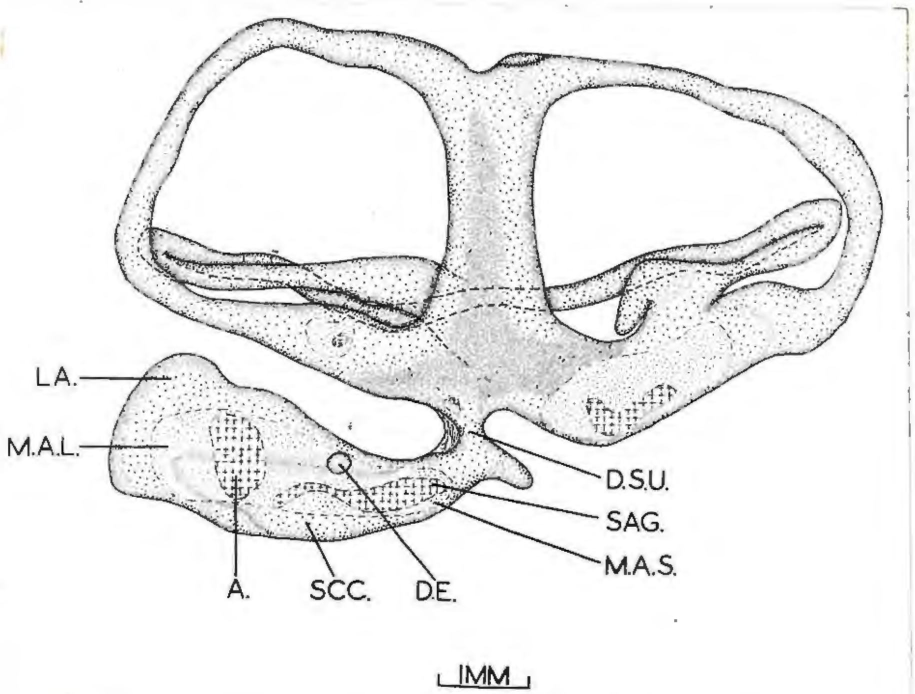

Fig. 2

Graphic reconstruction of the inner ear .

Medial view.

A., asteriscus ; D.E., ductus endolymphaticus ; D.S.U., ductus sacculo-utricularis ; LA., lagena ; M.A.L., macula acustica lagena ; M.A.S., macula acustica sacculi; SAG., sagitta; SCC., sacculus.

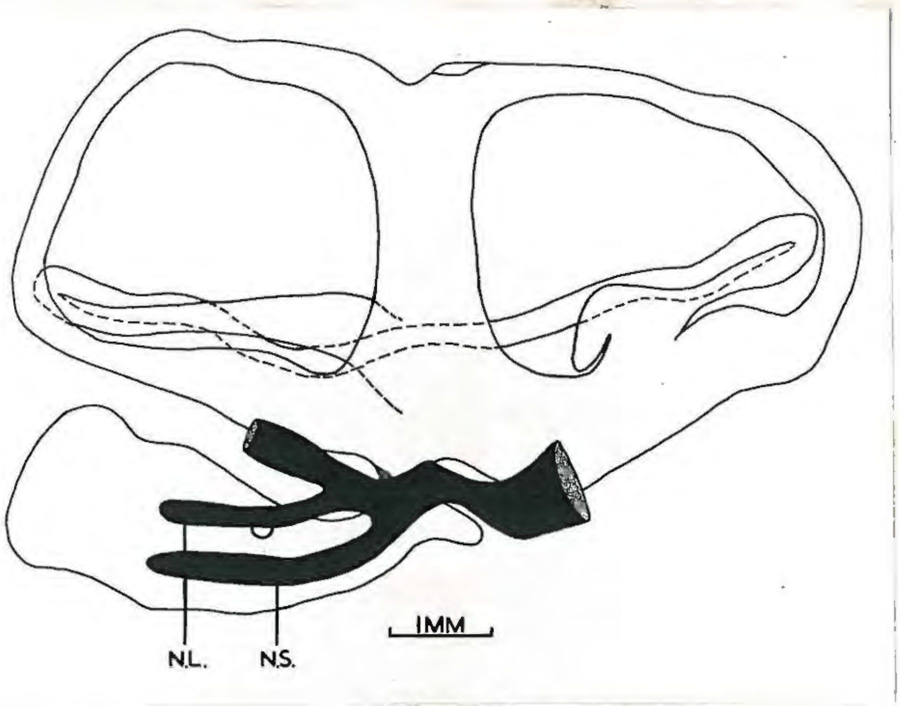

Fig. 3

Graphic reconstruction of the inner ear to show the innervation of the pars inferior.

Medial view.

N.L., n. lagenaris ; N.S., n. saccularis.

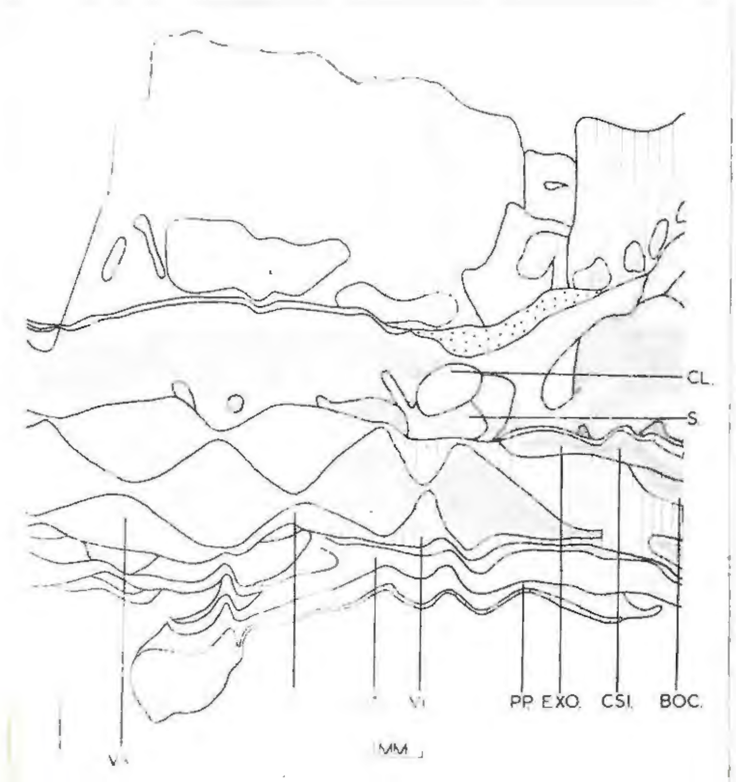

Fig. 4

Graphic reconstruction of the pars sustentaculum.

Internal view.

C.S.I., cavum sinus imparis ; D.A., dorsal aorta ; EXO., exoccipital ; P.P., pharyngeal process; Other abbreviations as in previous figures.

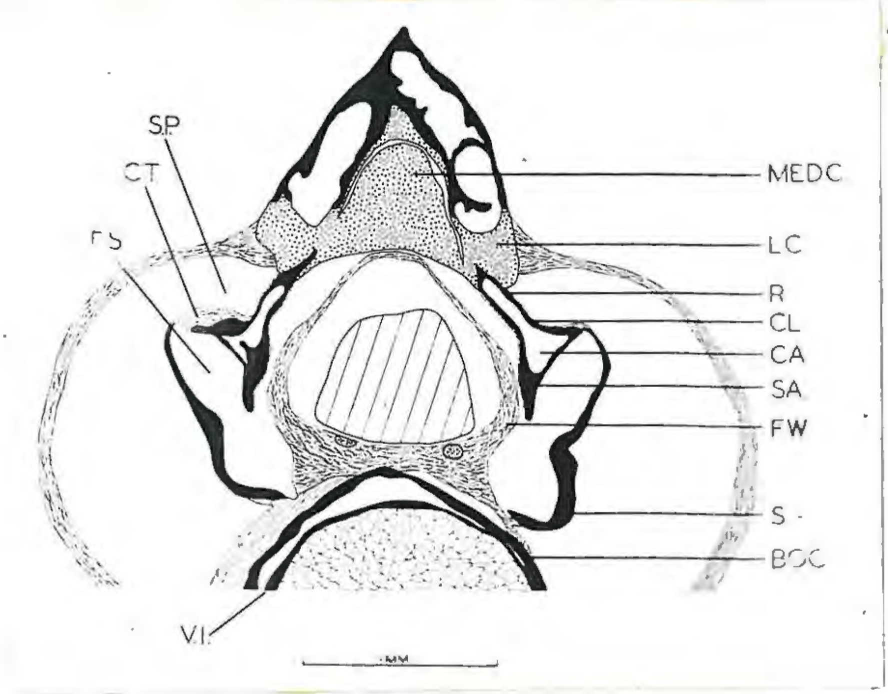

Fig.5

Transverse section through the region of the claustrum and scaphium.

CA., cavity ; C.T., connective tissue ; D.S., dorsal space ; F.W., fibrous wall ; L.C., lateral cartilage ; MED.C., median cartilage ; SA., saucer-shaped portion ; S.P., saccus paravertebralis. Other abbreviations as in previous figures.

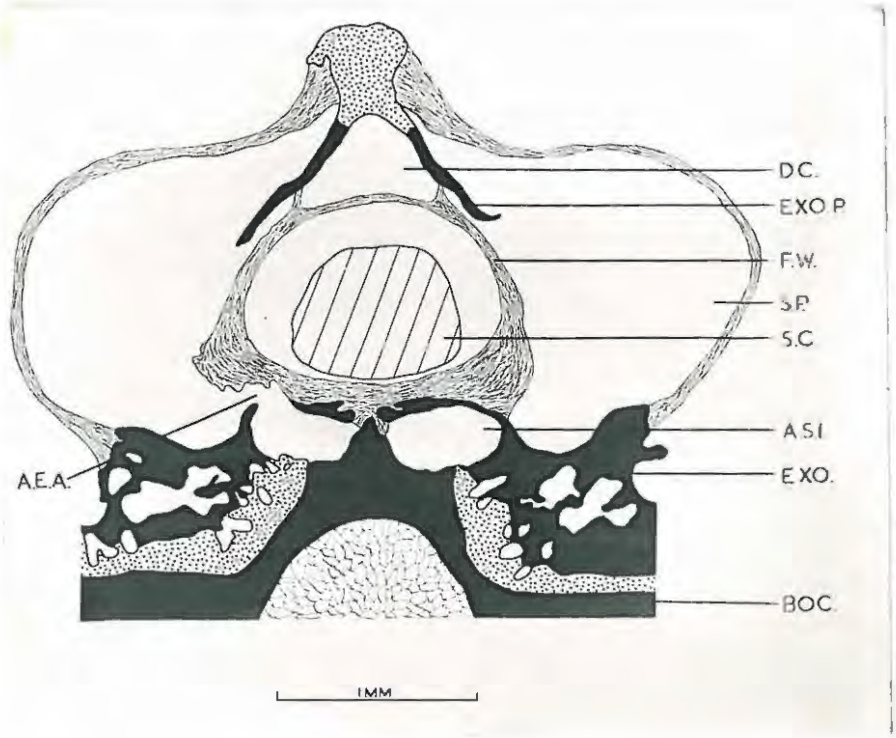

Fig. 6

Transverse section through the atrial cavities.

A.E.A., apertura externa atrii ; A.S.I., atrium sinus imparis ; D.C., dorsal cavity ; EXO.P., exoccipital plate ; S.C., spinal cord. Other abbreviations as in previous figures.

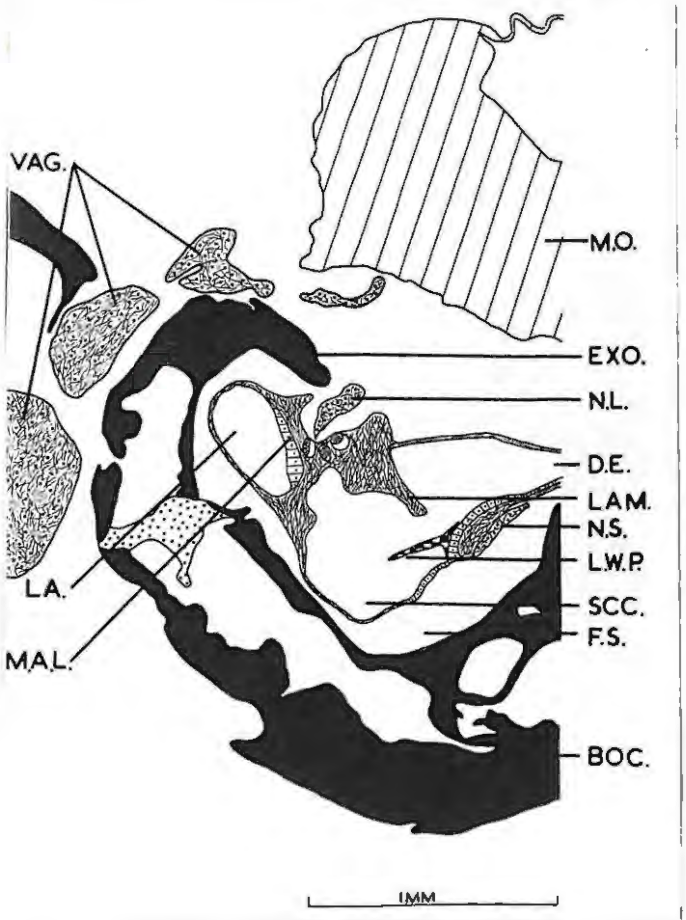

Fig. 7

Transverse section through the region of the ductus endolymphaticus and sacculus. F.S., fovea sacculi ; LAM., lamina ; L.W.P., lateral "wing"-like process ; M.O., medulla oblongata ; VAG., vagus nerve. Other abbreviations as in previous figures.

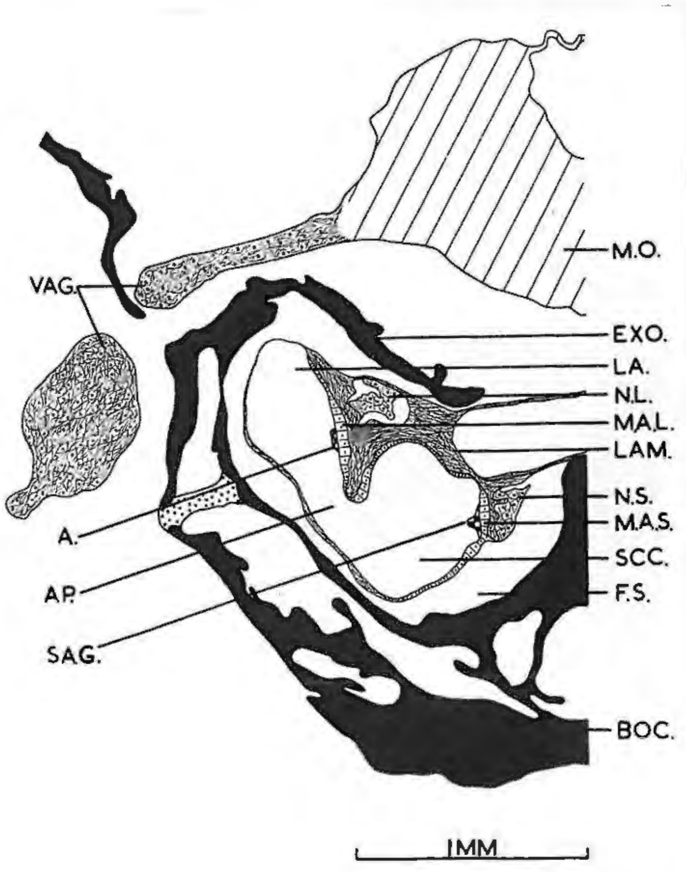

Fig. 8

Transverse section through the region of the sacculus and lagena.

AP., opening between lagena and sacculus. Other abbreviations as in previous figures.

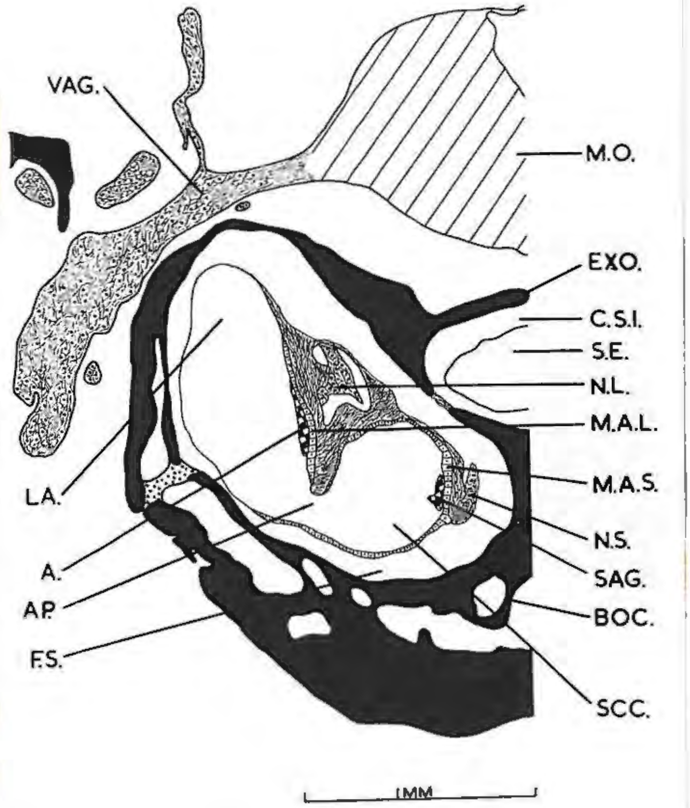

Fig. 9

Transverse section through the anterior region of the cavum sinus imparis.

S.E., sinus endolymphaticus. Other abbreviations as in previous figures.

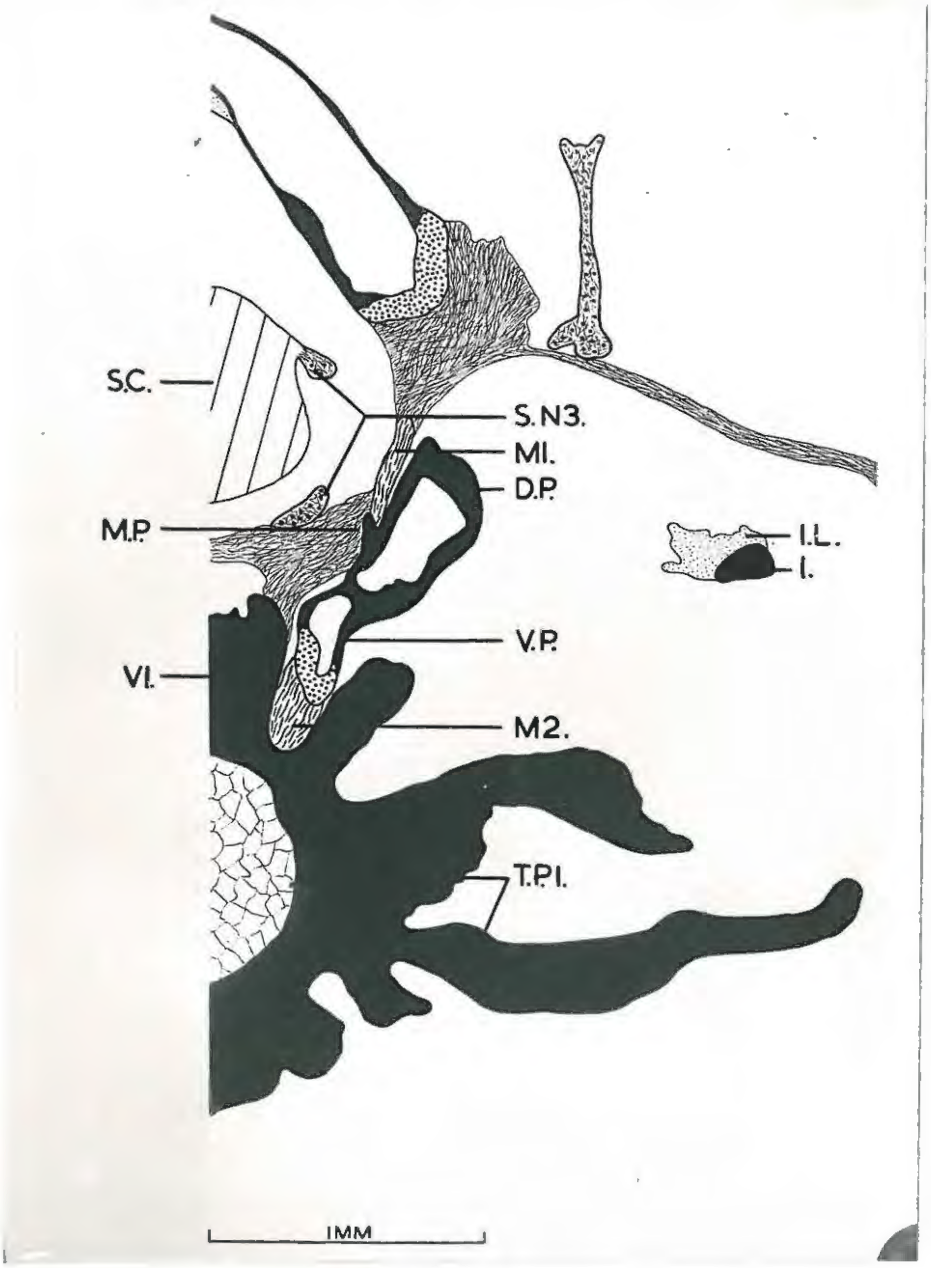

Fig. IO

Transverse section through the region of the scaphium showing the attachment of the two muscles.

MI., muscle ; M2., muscle ; M.P., medial process. Other abbreviations as in previous figures.

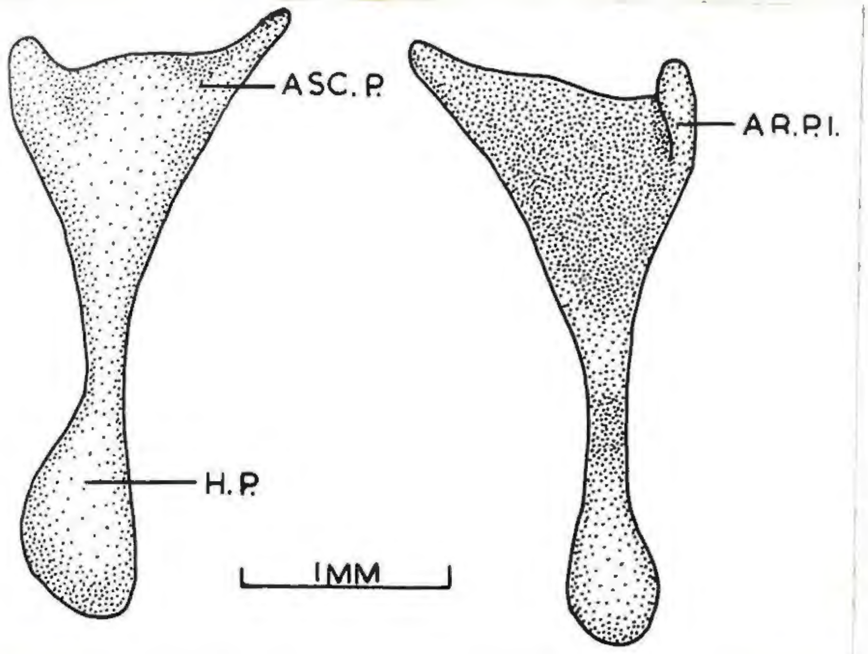

Fig. II

Diagram of the intercalarium.

AR.P.I., articular process of intercalarium ; ASC.P., ascending process ; H.P., horizontal process.

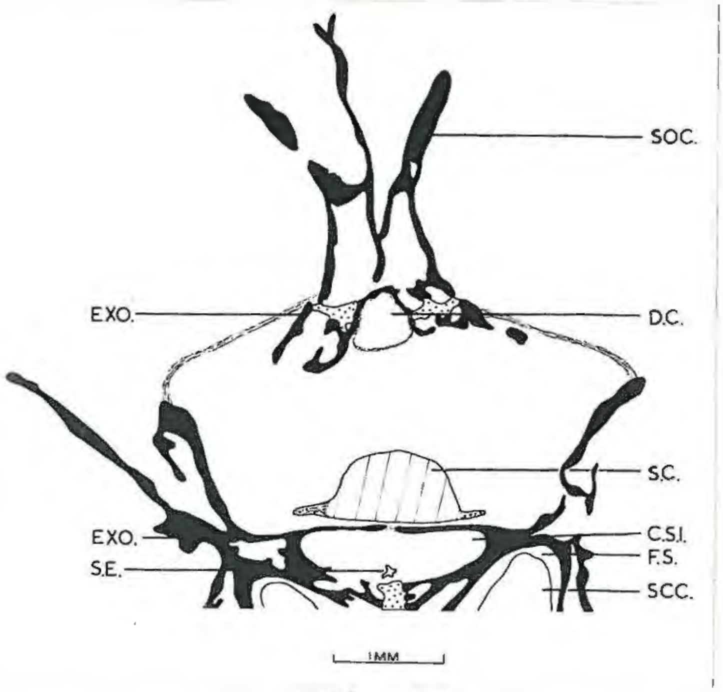

Fig. I2

Transverse section through the region of the dorsal cavity.

Abbreviations as in previous figures.

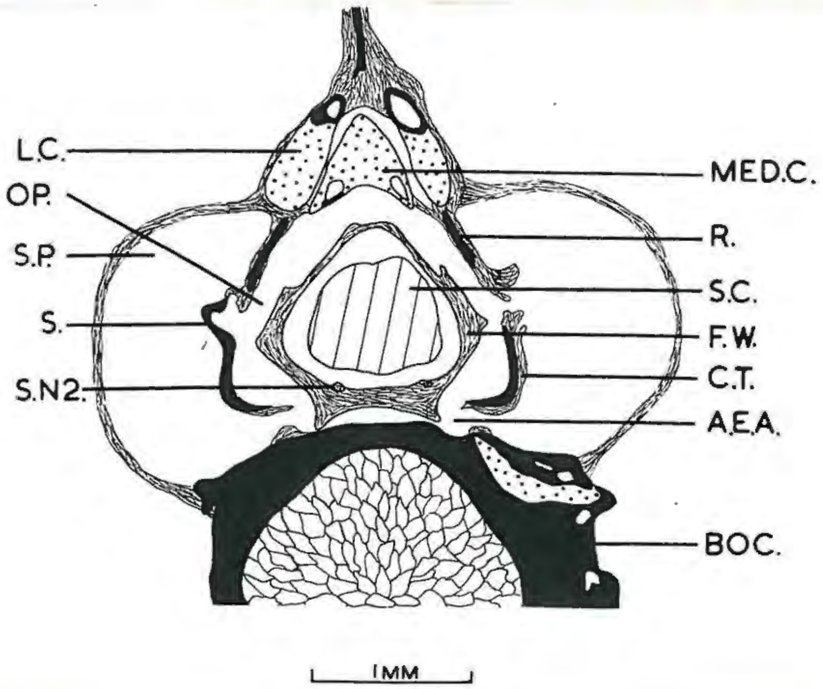

Fig. I3

Transverse section through the region of the claustrum and scaphium showing the lateral opening of the dorsal cavity.

OP., opening of dorsal cavity.
Other abbreviations as in previous figures.

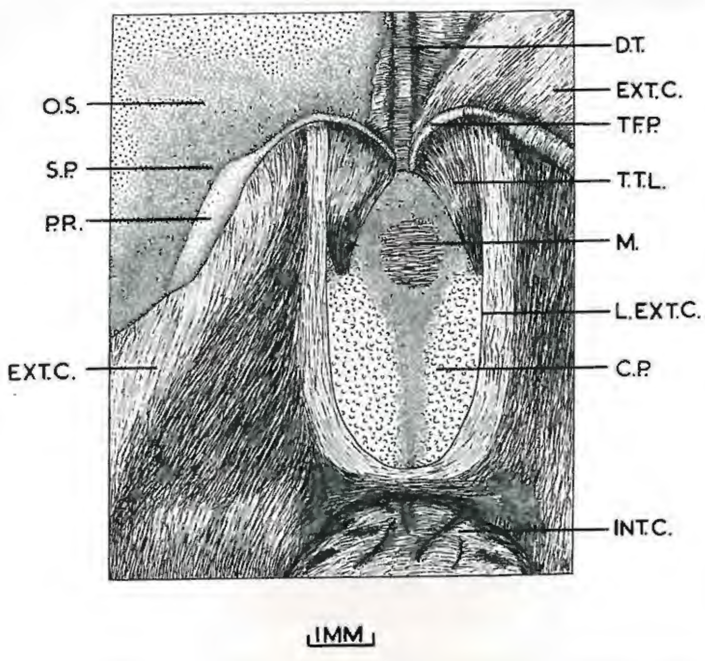

Fig. I4

Diagram of the attachment of the transformator process to the air-bladder and tensor tripodis ligament.

Posterior view.

C.P., central plate ; D.T., dorsal tendon of air-bladder ; EXT.C., external coat of air-bladder ; INT.C., internal coat of air-bladder ; L.EXT.C.; lateral margin of external coat ; M., membrane ; T.T.L., tensor tripodis ligament. Other abbreviations as in previous figures.