WEBERIAN APPARATUS IN MYSTUS GULIO (HAM-BUCH.) AND M. BLEEKERI (DAY)

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The present paper deals with the structural aspects of the Weberian ossicles and allied structures in two species of Mystus, namely, Mystus gulio and M. bleekeri. The treatment of this study involves an account of the anterior-most region of the vertebral column, the posterior region of the skull, the auditory apparatus, the Weberian ossicles, and the air-bladder. The first two regions are modified to form a supporting framework for the entire Weberian Mechanism.

(a) Mystus gulio (Ham-Buch.)

Anterior region of the vertebral column:

Six anterior vertebrae from 2nd to 7th are rigidly united to form a single compound vertebral region (Figs. 1, 2, 3). The second, third and fourth vertebrae are completely fused to form the so-called complex vertebra (Fig. 3, CV).

The ventro-lateral sides of the complex and the fifth vertebrae are invested by two superficial bones (Figs. 1, 2, 3, SB) one on each side. Each superficial bone (Figs. 2, 3, SB) is a triangular plate, the broad base of which is fused with the ventro-lateral side of the complex vertebra and the narrowed apex lies in contact with the ventral surface of the fourth transverse process. Each superficial bone extends forward up to the posterior face of the first vertebra where it gives rise to a ventral and anteriorly directed sub-vertebral process (Fig. 3, SVS) which in conjunction with similar articular processes of the first vertebra (AV1) and the basioccipital bone (APB) situated in front, gives rise to a sub-vertebral triangular plate on each side, at the junction of the vertebral column to the skull mid-vertically (Fig. 2). Posteriorly the superficial bone extends as far as the middle region of the fifth centrum. The superficial bone is produced vertically downwards in the form of a prominent ridge on each side of the compound vertebral region. The two-ridges thus...
form the lateral walls of a ventrally open groove—called the sub-centrum aortic groove (Fig. 1, AG). Ventrally this groove is covered by the median dorsal wall of the air-bladder.

Fig. 1. Ventral view of cranium and anterior vertebral region of *M. guile*. AG, Sub-centrum aortic groove. ATP₄, Anterior portion of the 4th transverse process. BO, Basioccipital. CG, Cardinal groove. EXO, Ex-occipital. PR, Prootic. PT, Pterotic. PTA, Ventral arm of the post-temporal. PP, Post temporal plates. PTP₄, Posterior portion of the 4th transverse process. RN, Radial nodule. RP, Ribbon-like “dorsal lamina”. SB, Superficial bone. SP, Sphenotic.

The first vertebra (Fig. 2, V₁) is a small discoidal bony piece, but without any rudiments of the transverse processes as in *Arius* (Karandikar and Masurekar, 1954). The ventral surface of this vertebra is produced downward into a pair of accessory articular processes (Fig. 3, AV₁). Anteriorly these frayed processes get interlocked with similar but stronger articular processes (APB) arising from the posterior ventral face of the basi-occipital. Posteriorly these processes get articulated with the forwardly directed, sub-vertebral processes given off from the superficial bones (SVS). This constitutes the first of the three points of attachment between the posterior face of the skull and the anterior vertebral region. All these articulations result
in the formation of a sub-vertebral triangular plate on each side of the dorsal aorta in that region. On the dorsal surface of the first vertebra are seen two cup-shaped sockets in which fit the rounded condylar or knob-like processes of the two "scaphia". The neural wall of this vertebra is made up of tough fibrous connective tissue (Fig. 3), extending between the foramen magnum and the anterior margin of the neural arch of the complex vertebra, on each side.

*The Complex vertebra* (Fig. 3, CV).—It is formed by the "complete" fusion of the 2nd, 3rd and 4th vertebrae. The neural spine of the third vertebra is a thin vertical triangular bony plate (Figs. 2, 3, NS₃), the broad base of which faces upwards. The anterior thickened end of this spine is bifurcated and clips the mid-dorsal ridge over the foramen magnum bounded by the ex-occipitals and the ventral plate of the supra-occipital. This is the second point of articulation between the skull and the compound vertebral region.

The posterior neural spine belonging to the fourth vertebra (NS₄) is inclined backwards in the caudal direction and is much longer than the third one. The first pterygiophore of the dorsal fin is inserted into the posterior groove of this neural spine.

The complex vertebra possesses two pairs of transverse processes. The anterior processes belonging to the third vertebra are modified into tripodes
Weberian Apparatus in Mystus gulio (Ham-Buch.) and M. bleekeri (Day) described later on (Fig. 1, TR). The transverse processes of the fourth vertebra are extensive (Figs. 1, 2, TP₄). Each process is divisible into an anterior portion (ATP₄) which is deeply arched and a posterior portion (PTP₄) which is more or less horizontal, by the presence of a deep semi-circular notch in its mesio-lateral side. This anterior portion (ATP₄) of each transverse process is greatly thickened and its anterolateral corner is produced into a claw-like process directed in the postero-lateral direction. At a short distance from the end of this claw there is an oval lateral articulating facet which is applied closely to a similar facet carried proximally by the ventral arm of the post-temporal bone, over the post-temporal plates (Fig. 4, FT). This is the third point of attachment between the skull and the compound vertebral region. The whole distal portion of this claw-like decurved process is movably applied to the ventral margin of the post-temporal plate on each side.

Fig. 3. Median longitudinal section of posterior cranium and anterior vertebral region. APB, Articular process of basioccipital. AV₁, Accessory articular process of the first vertebra. CSI, Cavum sinus imparis. CV, Complex vertebra. EXO, Ex-occipital. FS, Fovea sacculus. NC, Neural canal. NEXO, Intracranial neural extension of the exoccipital. NS, Neural spine. Sc, Scaphium. SOS, Supra-occipital shield. SVS, Sub-vertebral process of the superficial bone. UC, Utricular cavity. V, vertebra. Rest as in Figs. 1 and 2.

Along its dorsal edge, the superficial bone on each side is in contact with a thin ribbon-like bony process (Fig. 1, RP). This ribbon-like process arising from the underside of the 4th transverse process proceeds anteriorly over the crescentic process of tripus and terminates in the so-called radial nodule which is attached to the superficial bone on each side (RN). The ribbon-like process ("dorsal lamina") and the radial nodule together consti-
tute the "Os suspensorium" of many workers \(\textit{vide}\ \text{Karandikar and Masurekar, 1954}).

The superficial bones completely shield the lateral sides of the complex centrum, but the lateral surfaces of the fifth centrum are partly exposed owing to the reduction of these superficial bones to mere bony splints in that region (Fig. 2).

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**Fig. 4.** Posterior view of cranium. APB, Articular process of the basi-occipital. ATC, Atrial chamber. CLC, Clavicular cleft. EXO, Ex-occipital. EP, Epiotic. EXOP, Ex-occipital platform. FM, Foramen magnum. FT, Facet on the post-temporal stem for the articulation of the anterior portion of the 4th transverse process. PP, Post-temporal plate. PTA, Ventral arm of the post-temporal.

In their account of \textit{Macrones nemurus}, Bridge and Haddon (1893) state that the superficial bone on each side is continued posteriorly along the ventro-lateral sides of the centra as far back as seventh vertebral centrum. But the present observations on the two \textit{Mystus} species reveal that the superficial bone extends only up to the fifth centrum on each side. The ventro-lateral sides of the fifth centrum give rise to a pair of articulating ridges which extend backwards beyond the centrum. The superficial bone covering the complex vertebra on each side is attached to this ridge on each side of the fifth vertebral centrum. The sixth centrum also bears a similar pair of ventro-lateral ridges which extend beyond its anterior and posterior faces. The anterior extensions of these ridges articulate with the posterior extensions of the ridges of the fifth centrum. The posterior extensions of the sixth vertebral ridges cover the ventro-lateral sides of the seventh centrum. This interlocking between the superficial bones and these ridges is so perfect that one can easily mistake the superficial bones themselves extending up to the 7th centrum.
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A careful study of these superficial bones reveals that they are firmly fixed with the composite centrum of the complex vertebra and that no such fusion occurs in the case of first, fifth, sixth and seventh vertebrae of the compound vertebral region.

Karandikar and Masurekar (1954) in their description of \textit{A. platystomus} have pointed out that the close association of the superficial bone with the complex centrum, the bifid nature of the sub-vertebral process and the points of lateral fusion of the superficial bone indicate that the composite superficial bone may very likely be a special modification from the basapophyses of that vertebra (complex vertebra). In \textit{Mystus} the paired superficial bones are fused with the ventro-lateral sides of the complex vertebra. Similarly, the ridge-like processes present on the ventro-lateral sides of the fifth and sixth centra are also paired in nature. All these facts support the view that the superficial bones as well as the paired ridges on the fifth and the sixth centra, may probably be the modifications of the basapophyses of these vertebrae.

**Posterior region of the cranium:**

It is divisible into two parts—the \textit{occipital} and the \textit{otic}.

The \textit{occipital region}.—It consists of the supra-occipital, the two ex-occipitals and the basi-occipital. The \textit{supra-occipital} (Figs. 1, 4, SO) has its usual shape and articulations. It is produced posteriorly into a shield-shaped process (Figs. 2, 3). The \textit{ex-occipitals} (Figs. 1, 2, 4, EXO) situated around the foramen magnum also contribute to the formation of otic capsules. Each ex-occipital bone is continued inwards into the cranial cavity in the form of a vertical plate—\textit{the neural plate of the ex-occipital} (Fig. 3, NEXO) along the lateral side of the foramen magnum. The \textit{ex-occipital platform} (Fig. 4, EXOP) which forms the floor of the foramen magnum is formed by the horizontal extension of these neural plates along the median line and above the basi-occipital situated below.

The \textit{basi-occipital} (Figs. 1, 2, 3 and 4, BO) is dorsally excavated to form two deep lateral cavities and a medium groove situated at a little higher level than the former. They are covered dorsally by the ex-occipital platform (Fig. 4, EXOP). The lateral cavities are then called as \textit{fovea sacculi} (Fig. 3, FS) in which the sacculi of the inner ears are lodged. The median groove called as \textit{cavum sinus imparis} (CSI) lodges the common sinus endolymphaticus of the inner ears. Anteriorly it communicates with the auditory cavities, and opens posteriorly into an extra cranial atrial chamber (Figs. 4, 5, ATC), situated between the floor of the foramen magnum and the posterior dorsal part of the basioccipital. The \textit{atrium} is single and not double as described
by Bridge and Haddon (1893). The fibrous membrane forming the wall of the atrium is perforated laterally by an oval aperture on each side. To the rim of the aperture is attached by membrane, the spatulate process of Scaphium—the second Weberian ossicle, like a movable shutter.

The otic region.—The otic capsules are not so prominent externally. The large utricular cavities (Fig. 3, UC) communicate with the general cranial cavity by large openings each bounded anteriorly by a ridge on the prootic (PR) and posteriorly by the intra-cranial neural plates of the ex-occipitals (NEXO). The bones that take part in the formation of the otic capsules are the prootics (Figs. 1, 3, PR), the epiotics (Fig. 4, EP), the pterotics (Figs. 1–3, PR), the sphenotics (SP) and the ex-occipitals. It is surprising that the supratemporal (Fig. 2, ST) bone which is present here, as well as in any other siluroid species is not mentioned by Bridge and Haddon (1893) in their account of Macrones nemurus and other species. The post-temporal (Fig. 1, PTM) is V-shaped with dorsal and ventral arms. Both these arms unite in the postero-lateral...
corners of the cranium to form a triangular plate-like structure called the *post-temporal stem*. Ventrally this post temporal stem on each side gives rise to a thin, large semi-circular plate called the *post-temporal plate* (PP). On the concave posterior face of this plate and near its proximal end there is a vertically disposed facet (Fig. 4, FT) which is applied to the claw-like curved extension of the fourth transverse process on each side.

**The auditory apparatus:**

The auditory apparatus on each side (Fig. 5) consists of three semi-circular canals, utriculus, sacculus and ductus endolymphaticus.

The *utriculus* (UT) is a large sac containing a pearly white otolith and lodged freely in the otic capsule. The *sacculus* (SCS) is lodged in the fovea sacculus situated below the ex-occipital platform. It is connected with the utriculus by a short narrow tube called the *ductus sacculo-utricularis* (DSU). Attached to the sacculus and in communication with it on the inner side is the small *lagena* (LG). Both contain white otoliths. From the anterior side of the sacculus arises the short *endolymphatic duct* (ED). It joins the corresponding one from the opposite side, thus forming the transverse ductus endolymphaticus. From the point of junction arises a thin-walled sac the *sinus endolymphaticus* (SE) lodged within the cavum sinus imparis situated between the foveae sacculi. All these parts of the auditory organ are filled with endolymph, while the otic cavity, the foveae sacculi and the cavum sinus imparis contain perilymph. The cavum sinus imparis communicates with the extra cranial atrium (ATC) by a narrow aperture. The atrium also is filled with lymph which is continuous with the perilymph surrounding the various parts of the auditory organs. The spatulate process of scaphium (SC) the second Weberian ossicle which closes the lateral aperture in the atrium on each side is thus in contact with the lymph.

**The Weberian ossicles:**

They are four on each side, namely, the claustrum, the scaphium, the intercalarium and the tripus. The claustrum, however, is not directly connected with the chain of the other three ossicles situated laterally on each side of the anterior region of the vertebral column.

The *claustrum* (Fig. 6 a) is a thin flattened rod-like bone embedded in the fibrous neural wall of the first vertebra on each side, just above the closed atrial cavity. The claustra are said to be homologous with the bifid neural spine of the first vertebra.

The *scaphium* (Fig. 6 b) consists of a horizontal spatulate process (SPS) and an elongated vertical process (VPS) lying in the fibrous neural wall of
first vertebra behind and parallel to the clastrum, on each side. The concave inner surface of the spatulate process of the scaphium which extends forward, is fitted against the lateral window of the atrial cavity by means of a loose membrane thus permitting the ossicle to perform a little sideway movement, thereby causing a change in the volume of the atrial cavity. At the angle of the vertical and the spatulate process is a prominent rounded kondyle (AKS) which rotates sideways in the socket on the dorso-lateral side of the first vertebral centrum, on each side. Morphologically the scaphium is said to represent the neural arch of the first vertebra on each side.

The *intercalarium* (Fig. 6 c) consists of a small discoidal bony piece embedded in a ligamentous band connecting the outer side of the spatulate process of the scaphium and the anterior end of the tripus (Fig. 5). Bridge and Haddon (1893) in their description of *Macrones nemurus* mention that the intercalarium, like the scaphium, consists of two parts: a disc-like piece embedded in the inter-ossicular ligament, and a small vertically directed process which is embedded in the fibrous neural wall of the first vertebra.
The tripus is the largest of all the ossicles (Fig. 6-d, e). It consists of a proximal stem called as the articular process of tripus (TRS), which broadens out distally into an anterior triangular process (TRA) and a posterior crescentic process (TRC). The tripus is slightly movable in a lateral plane with the articular stem acting like a fulcrum. It is this ossicle which plays an important role in the physiology of the Weberian apparatus. The crescentic process is thin, flattened and slender. Its distal end is in contact with the lateral side of the superficial bone, at about the middle of the complex centrum. From the point where the crescentic process begins to curve inwards towards the superficial bone, there extends transversely a slender buttress-like process (BT) towards the lateral side. The whole crescentic process together with its buttress-like projection is embedded in the dorsal wall of the air-bladder. A thickened ventral ridge (VT) arises from the base of the buttress-like process and extends obliquely inwards towards the articular process of the tripus.

The anterior process of tripus, the spatulate body of scaphium and the intercalarium, all are enclosed in a fluid filled fibrous sac called the saccus paravertebralis situated on either side of the atrial cavity.

The homologies of these ossicles have been described by Karandikar and Masurekar (1954).

The air-bladder:

The air-bladder (Fig. 8) is cordate in shape and is situated below the vertebral column. The subvertebral triangular plates, the post-temporal plates and the claw-like tips of the 4th transverse processes are firmly applied against the anterior wall of the bladder. Posteriorly the bladder extends up to the 10th vertebra. The bladder is narrowed and rounded behind. Dorsally it is in contact with the superficial bones and the fourth and the fifth transverse processes. Ventrally, the bladder is invested by the peritoneal sheets. On the anterior face of the bladder there is a pair of transverse septa. Each septum is attached mesially to the sub-vertebral articular process of
the superficial bone and laterally to the ventral margin of the post-temporal and the claw-like distal extremity of the 4th transverse process. The fibres of this septum on each side blend with the ligamentous fibres by means of which these latter two skeletal elements are attached to each other. Dorsally the septum is attached to the anterior margin of the fourth transverse process.

A narrow tube called the *ductus pneumaticus* arises from the ventral side of the anterior portion of the bladder and communicates with the oesophagus. The body skin comes in contact with the anterolateral corners of the air-bladder, forming what are called as *lateral cutaneous areas* (LCA) which are extensive.

The walls of the air-bladder are perfectly smooth and comparatively thin and translucent. Internally the air-bladder (Fig. 8) is divided into
number of compartments by fibrous septa running transversely and longitudinally. A primary transverse septum (PTS) divides the cavity of the bladder into an anterior chamber and a posterior chamber. A longitudinal septum (MLS) divides the posterior chamber into two lateral compartments which are subdivided into many chambers by four to five secondary transverse septa (STS) gradually diminishing in size. Numerous fibrous props support the various internal septa.

The cavity of the anterior chamber is greatly constricted in the middle by the presence of the subvertebral superficial bony keel (SB) and a pair of longitudinal fibrous ridges along the inner side of the midventral wall of the bladder in that region. The anterior chamber is then divisible into right and left halves. The midventral longitudinal ridges bend upward and are attached to the radial nodules where they form the “anterior pillars”. The primary transverse septum is thickened laterally to form posterior pillars attached to the posterior margins of the fourth transverse processes.

Histologically, the wall of the air bladder is composed of two layers—the membranous tunica interna and the fibrous tunica externa. The tunica interna forms an internal lining to the various chambers. The mid-dorsal part of the tunica externa of the bladder in contact with the superficial bones is reduced to a thin membrane.

The tunica externa is composed mainly of tendon-like fibres which are arranged in two layers or strata the outer and the inner. The fibres of both these strata in the anterior chamber are inserted into the outer convex margin of the crescentic process of the tripus on each side. Between the radial nodule and the inner margin of the crescentic process on each side stretch certain radial fibres which presumably belong to the inner stratum.

The variations in the size of the air-bladder to adjust itself to the various conditions of hydrostatic pressure during ascent or descent of the fish in the water are presumably conveyed to the brain by the chains of Weberian ossicles to the atrial lymph which is in contact with the inner face of the spatulate scaphium. From there by means of waves arising in the perilymph the sensation is conveyed to the endolymph of sinus and ductus endolymphaticus and ultimately the stimulus is passed on to the auditory nerve.

The Weberian apparatus thus probably acts as a pressure register serving to acquaint the fish with the varying degrees of tension of gases to which the air-bladder is subjected due to variation in the hydrostatic pressure during vertical locomotion of the fish in water.
It resembles *Mystus gulio* in almost all features. Even in this freshwater species the intercalarium (Fig. 7 a) has the usual disc-like shape and is embedded in the interossicular ligamentous band. At least in *Mystus gulio* and in *M. bleekeri*, there is no intercalarium with an additional vertical process embedded in the fibrous neural wall of the first vertebra, as is the case described by Bridge and Haddon (1893) in *Macrones nemurus*. The other ossicles are similar to those of *M. gulio* (Fig. 7 b, c).

The air-bladder is cordate in shape and bulging dorsoventrally. The walls are extremely thin and transparent. There is only one transverse septum and that is primary. Numerous fibrous ridges are present on the primary transverse and longitudinal septa. Other features are similar to those of *M. gulio*.

**SUMMARY**

An account of the Weberian Apparatus in two species of *Mystus*, namely, *M. gulio* and *M. bleekeri*, has been given. In this connection, the anterior region of the vertebral column, the posterior region of the cranium, the Weberian ossicles, the internal ears, and the air-bladder have been studied in detail.

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