VII. "Contributions to the Anatomy of Fishes. I. The Air-bladder and Weberian Ossicles in the Siluridæ." By

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Weber, in his classical memoir entitled 'De Aure et Auditu Hominis et Animalium. Pars. I.—De Aure Animalium aquatilium,' published in 1820, was the first to show that in certain families of Physostomous Teleostei, which were subsequently grouped together under the name of Ostariophyseæ by the late Dr. Sagemehl, there exists a peculiar connexion between the membranous labyrinth of the internal ear and the air-bladder by means of a chain of movably interconnected "auditory" ossicles. Of the four families (Gymnotidæ, Characinidæ, Gymnarchidæ, and Siluridæ) in which this singular mechanism is present, the Siluridæ have received but comparatively scanty attention since the publication of Weber's paper. Weber himself only described the air-bladder and auditory ossicles of one species (*Silurus glanis*). Johannes Müller, in his various communications to the Berlin Academy during the years 1843–45, added somewhat to our knowledge of these structures, and notably by his discovery of the *springfederapparat*; but Müller's attention was mainly directed to the grosser features in the anatomy of the air-bladder to the entire exclusion of all but the slightest reference to the important skeletal modifications which are associated with the peculiar structure of that organ in the Siluridæ. Reissner has given a fairly complete account of the bone-encapsuled air-bladder of *Rhinelepis*, but by far the most valuable of the more recent contributions to this branch of vertebrate morphology are the papers by Professor Ramsay Wright, relating to the aberrant Siluroid *Hypothalmus*, and to the more normal North American species, *Amiurus catus*. In his papers on *Amiurus*, Professor Wright was not only the first to describe the fusion of the second, third, and fourth vertebræ in the formation of what we have termed the "complex vertebra"—a fact which could hardly have been discovered except through embryological evidence—but was also the first to give an accurate account of the skeletal relations and attachments of the air-bladder in any one Siluroid.

In this preliminary communication we propose to state briefly the results of our investigations into the various modifications which the air-bladder and the "auditory ossicles" undergo in ninety-two

species of Siluridæ, referable to about fifty genera, and mainly belonging to Dr. Günther's sub-families of Siluridæ Homalopteræ, S. Heteropteræ, S. Proteropteræ, and S. Proteropodes. For the present we shall only give a brief *résumé* of the morphological variations in the structures concerned, leaving their physiological bearing and the more general conclusions which the facts elucidated suggest, to a future and more detailed communication to this Society; but before doing so we venture to suggest the need of a revision of the customary nomenclature of the so-called "auditory ossicles." From a mistaken idea of their homology with the Mammalian auditory ossicles, Weber gave to three of them the suggestive but extremely misleading names of "incus," "malleus," and "stapes." Since Weber's time, however, it has become obvious that the "auditory" ossicles of the Ostariophyseæ are in no sense homologous with the similarly named bones of the Mammalian tympanum, and it is almost equally clear that the two series of ossicles have nothing in common with regard to their respective functions. With a view of avoiding all possibility of the confusion which may result from applying identical terms to structures widely different in origin and probably equally remote in function, we venture to suggest a different nomenclature for the "auditory ossicles" of Weber. 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. The fourth ossicle, called the "claustrum" by Weber, forms one of the series of auditory ossicles in the Cyprinoid fishes, but has no such physiological significance in the Siluridæ, although it is very generally present. As the name "claustrum" is open to none of the objections which can reasonably be urged against the retention of Weber's nomenclature of the three preceding ossicles, it may with advantage be retained. For the ossicles collectively, including the claustrum, and for obvious reasons, we would suggest the name "Weberian ossicles" as an appropriate designation, instead of "auditory ossicles."

In summarising the more noteworthy of the results of our investigations into the morphology of the air-bladder and Weberian ossicles, and the correlated modifications which the anterior vertebræ and their processes undergo, we may indicate, in the first instance, such features as appear to be common to nearly all Siluroids, and secondly, those that are characteristic of particular genera or species.

Although only demonstrated in one particular instance (the young of *Amiurus catus*) by Ramsay Wright, our researches lead us to

believe that 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 vertebræ indistinguishably combined to form an apparently single vertebra, for which we venture to suggest the name of "complex vertebra." The discovery by Baudelot that the "complex vertebra" of the Cyprinidæ was formed by the fusion of the second vertebral centrum with the third vertebra, was due to the distinctness of these elements in one particular species, but no evidence of a similar nature is available in any but embryonic Siluridæ. In no adult Siluroid is there the slightest trace of intervertebral spaces or sutures between the three confluent centra, in fact, the only features which in any way suggest the composite nature of the complex vertebra in that family are the perforation of its neural arch by two pairs of spinal nerves and the occasional presence of two pairs of nutrient foramina on the ventral surface of its centrum. This fusion of vertebræ in the formation of the "complex" is almost invariably attended by the partial anchylosis of the latter to the fifth vertebra, partly as the result of the firm sutural union of their correlated elements, and in part due to the investment of the lateral surfaces of their centra by a continuous deposit of superficial bone. Moreover, the conjoined vertebræ, with the addition of the centrum of the first, are so articulated to the skull that little, if any, motion is possible, either between the individual vertebræ or between the latter and the skull. The centrum of the first vertebra is nearly always more or less rudimentary.

With the possible exception of the claustra no distinct or ossified intercalary elements are ever present.

The first vertebra very rarely has transverse processes, and even when present (*e.g.*, some species of *Arius*) they are extremely rudimentary. The transverse processes of the fourth vertebra, on the contrary, are always greatly expanded, not infrequently divided into anterior and posterior division by a cleft, and with or without the aid of those belonging to the fifth vertebra form a more or less complete investment to the dorsal and anterior walls of the air-bladder. The sixth is, as a rule, the first rib-bearing vertebra; exceptionally, however, it may be the fifth (*Callichrous*), or even the seventh (*Clarias*).

In almost all cases, except where they are modified to form an "elastic-spring-apparatus," the transverse processes of the fourth vertebra, in addition to their characteristic relations to the air-bladder, form a more or less rigid support to the proximal elements of the pectoral girdle.

Over a somewhat triangular area, on each side, between the exoccipital in front and the anterior margin of the arch of the complex vertebra behind, the wall of the neural canal is formed only by fibrous

membrane, in which the claustrum and the ascending process of the scaphium are imbedded.

Of the four Weberian ossicles the claustrum has no physiological relations to the atrial cavities (*atria sinus imparis* of Weber), but merely strengthens the wall of the neural canal behind the exoccipital. Each scaphium has a spatulate process which fits into and completely closes the corresponding external atrial aperture, and at the same time forms the outer wall of the atrial cavity of its side, and also a rounded condylar process for articulation with the centrum of the first vertebra. The intercalarium is usually represented by an elongated or discoidal nodule imbedded in the stout ligament ("interossicular ligament") connecting the scaphium with the tripus, and even if horizontal and ascending processes are present, the ossicle never articulates with the centrum of the second vertebra to which, as a modified neural arch, it belongs. The tripus is always a tripartite ossicle with its posterior or crescentic process imbedded in the dorsal wall of the air-bladder; the anterior process is directed forwards parallel to the long axes of the complex and first centra, and opposite the external atrial aperture of its side is connected by the transversely-disposed interossicular ligament with the convex outer surface of the spatulate process of the scaphium. The articular process usually articulates with the lateral surface of the vertebral centrum (the third), of which it is a modified transverse process; very rarely (*e.g.*, *Auchenipterus*) is the process directly continuous with the neural arch.

The Weberian ossicles, or at all events the free portion of the tripus and the intercalarium, are enclosed within a membranous saccus paravertebralis, the anterior wall of which is perforated by the interossicular ligament as the latter passes forwards from the tripus to its attachment to the scaphium. Unlike the Cyprinidæ, the complete closure of the external atrial aperture by the spatulate process of the scaphium and the minute size of the hypoglossal foramen in the Siluridæ completely cut off all communication between the cavity of the saccus and the cranial cavity.

The first spinal or hypoglossal nerve perforates the exoccipital. The second and third spinal nerves emerge from the neural canal between the claustrum anteriorly and the arch of the complex vertebra behind, but are invariably separated by the ascending process of the intercalarium whenever that process is developed, as in *Macrones*, *Liocassis*, and *Bagroides*. The fourth and fifth spinal nerves traverse the neural arch of the complex vertebra, and the sixth, the arch of the fifth vertebra. The additional spinal nerve described by Sagemehl in *Silurus glanis* as emerging between the claustrum and the ascending process of the scaphium, we have never met with, although our attention has been specially directed to that point.

The air-bladder varies greatly in degree of development, not only in different genera, but in different species of the same genus. Even individual variations are not infrequent. Very rarely does it exhibit the bipartite division into an anterior and a posterior sac so characteristic of other families of Ostariophyseæ. One of its most noteworthy features is a tendency to lateral development, whereby the outer walls of the anterior portion become applied, through the divergence of the dorso-lateral and ventro-lateral muscles of the body wall, directly to the external skin ("lateral cutaneous areas"). 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 Siluridæ, or into the corresponding walls of the laterally situated air-sacs in the abnormal forms, and takes place in such a way that the fibres forming the anterior and lateral walls of each half of an anterior chamber, or of each air-sac, converge as they pass into and form the dorsal wall, and ultimately become inserted into the convex outer margin of the tripus of that side. Specialised fibres of the dorsal wall ("radial fibres") converge like the radii of a circle from the inner concave margin of the crescentic process, and are inserted either directly into the adjacent lateral surface of the complex centrum or indirectly through the intervention of an osseous nodule ("radial nodule"). Except, perhaps, in cases where the same effect is produced by their partial encapsulation by bone, the anterior chamber of the bladder, and its equivalent the laterally-situated air-sacs of the abnormal Siluridæ, generally have their walls so attached to, or buttressed by, rigid portions of the axial skeleton, that only their outer or lateral walls are capable by inward or outward bulging of allowing variations in the internal capacity of the bladder to take place.

A ductus pneumaticus is very generally, but not invariably, present.

In nearly all Siluroids the lateral growth of the air-bladder, and the intimate relation of its outer walls to lateral cutaneous areas, have led to the displacement of the lateral lobes of the liver and their enclosure within peritoneal *cul-de-sacs*—a condition which usually persists even in cases where the air-bladder has undergone partial atrophy.

In many of the features to which reference has just been made, the Siluridæ differ from all the other families in which a Weberian mechanism is present.

As a convenient means of summarising the more important generic and specific variations, the Siluroids may be somewhat arbitrarily divided into two principal groups:—(I) the *Siluridæ normales*, and (II) the *Siluridæ abnormales*. In the former group the air-bladder is always well developed and subdivided internally into three inter-

communicating compartments, of which one is anterior and two posterior or lateral in position. The anterior and dorsal walls of the anterior chamber may be more or less completely invested by the modified transverse processes of the fourth and fifth vertebræ, but the latter do not form deep concave recesses or capsules for the partial or complete enclosure of the entire air-bladder.

In the Siluridæ abnormales on the contrary, the air-bladder is always small relatively to the size of the Fish, and more or less degenerate, sometimes partially solid, but almost invariably includes two laterally situated air-sacs with simple cavities, which together may be regarded as equivalent to the anterior chamber of a normal Siluroid. Lateral compartments, as a rule, are absent altogether, or, if present, are very rudimentary. Whatever its condition, the air-bladder is almost always partially or completely enclosed within transversely disposed bony recesses, formed either by the transverse processes of the fourth vertebra alone, or in conjunction with those of the fifth vertebra.

Although a convenient method of classifying morphological facts, it is obvious that this classification, based as it is upon so variable an organ as the air-bladder, can have no genetic value.

(I.) *Siluridæ Normales.*

Under this head may be included such genera as :—*Plotosus*, *Wallago*, *Callichrous*, *Cryptopterus* (certain species). *Eutropius*, *Pangasius*, *Macrones*, *Rita*, *Pimelodus* (certain species), *Piramutana*, *Arius*, *Osteogeniosus*, *Oxydoras*, *Malapterurus*, and others.

In the Siluroids included in this group the number of rigidly interconnected vertebræ varies. The first, the complex, and the fifth vertebræ are almost invariably so connected together that no motion is possible between them, and occasionally the sixth, the seventh, and even the eighth may be included in the series. The rigidity of the complex and fifth vertebræ, with the occasional addition of the sixth, may be further increased by the sutural union or partial anchylosis of their respective transverse processes. The anterior vertebræ are also firmly connected to the skull, generally by the articulation of the arch and spine of the third vertebra with the exoccipitals and supraoccipital, the transverse processes of the fourth vertebra with the post-temporals, and the spinous processes of the third and fourth vertebræ with the supraoccipital spine ; less frequently by the formation of interlocking accessory articular processes on the contiguous ventral margins of the basioccipital and the centra of the first and complex vertebræ (*Macrones*, *Bagrus*). In *Arius* the accessory processes are very strongly developed, and by their downward growth and coalescence, form a stout, conical subvertebral process for the

attachment and support of the anterior wall of the air-bladder. In some Siluroids the connexion of the skull with the anterior vertebræ may be rendered still more intimate by the articulation of the supra-occipital spine with the expanded dermal plates of the first and second interspinous bones, as in *Auchenipterus*, *Oxydoras*, &c., or even by the downward growth of paired processes from the supraoccipital to unite with the dorsal surfaces of the transverse processes of the fourth vertebra, as in *Arius*, *Batrachocephalus*, &c.

The centrum of the first vertebra varies greatly in size, but is always the smallest of the anterior vertebræ. Two pit-like sockets are always found on its dorsal surface for the reception of the globular condylar processes of the scaphia. The complex and fifth centra are the largest, or, at all events, the longest of the anterior vertebræ, and, as a rule, their anterior and posterior concavities are unsymmetrically developed. In nearly all cases these centra are not only elongated but laterally compressed, so as to form a prominent subvertebral keel, which gives rise to a deep groove along the medio-dorsal line of the anterior chamber of the air-bladder, and, at the same time, internally, to a prominent longitudinal ridge, partially subdividing the cavity of the chamber into two laterally bulging halves. A fan-shaped subvertebral process may be developed from the ventral and anterior margin of the complex centrum for the support of the anterior wall of the bladder (*e.g.*, *Auchenaspis*), and the lateral surface of the same centrum is not infrequently thickened into oblique lateral ridges for the dorsal attachment of the anterior pillars of the anterior chamber. For the same purpose a variously shaped osseous nodule ("radial nodule") is attached to the dorsal extremity of each ridge, or in its absence directly to the centrum, and is either confluent therewith, or suturally, or by fibrous tissue only, connected thereto. The radial nodules in addition to serving for the attachment of the "anterior pillars" receive also the insertion of the radial fibres of the tripus. Almost invariably a thin slender lamina of bone, the "radial ridge," is prolonged from each radial nodule, and, after passing obliquely upwards, outwards, and backwards, ventral to the posterior cardinal vein, blends with the ventral surface of the transverse process of the fourth vertebra.

The neural arch of the complex vertebra is partially or completely anchylosed to the arch of the fifth vertebra, which, in turn, may be similarly connected with the arch of the sixth vertebra, or the rigid union of the different neural arches may be effected by a firm sutural union.

The transverse processes of the fourth vertebra, very frequently those of the fifth vertebra, and more rarely those belonging to the sixth vertebra (*Platystoma*), are more or less expanded, and by their partial anchylosis or sutural union with one another, form on each

side of the vertebral column a broad, wing-like plate of bone, the anterior margin of which is strongly decurved, for the investment of the dorsal and anterior walls of the anterior chamber of the air-bladder. The transverse process of the fourth vertebra has a broad flat root, and may be simple, or, as is more usually the case, cleft more or less deeply into anterior and posterior divisions, of which the former is always decurved for a portion of its extent, and closely applied, even if not attached, to the lateral portion of the anterior wall of the bladder, in addition to its ligamentous or articular connexion with the post-temporal. In certain Siluroids the transverse process becomes modified to form the "elastic-spring-apparatus," first described by Johannes Müller. In some of these forms (*Malapterurus*, *Synodontis*, *Pangasius*) each anterior division is almost completely separated from the posterior division, with an oblique origin from the arch of the complex vertebra, and, becoming flexible and highly elastic, expands distally into a more or less oval plate, which is closely applied to the lateral portion of the anterior wall of the bladder. In others (*Auchenipterus*, *Oxydoras*) the anterior division also forms an "elastic-spring-apparatus," but the posterior division is entirely wanting. In all such cases the modified transverse processes are provided with powerful protractor muscles, which have their origin on the posterior face of the skull, and their insertion into the anterior surfaces of the oval plates.

The post-temporal bone always has a transversely, or obliquely, disposed inferior limb for articulation at its inner extremity with the lateral surface of the basioccipital, in addition to an ascending process for articulation with the pterotic and epiotic bones. Where the transverse process of the fourth vertebra fails to articulate with and support the post-temporal, as is the case in all Siluroids possessing an "elastic-spring-apparatus," the inferior limb of the latter is exceptionally massive, with an extensive articulation, or even partial anchylosis, with the basioccipital or, in addition, with the exoccipital also. In other genera (*Macrones*, *Bagrus*, &c.) the inferior limb, in conjunction with the body of the same bone, may form a bony expansion or post-temporal plate, which, with the produced crescentic distal extremity of the anterior division of the transverse process of the fourth vertebra, forms a slightly concave bony structure for the support of the lateral portion of the anterior wall of the bladder. From being but faintly concave on its posterior face, the post-temporal plate and the adjacent portion of the inferior limb may become deeply excavated to form a goblet-shaped cavity, into which a thin-walled cœcal diverticulum of the air-bladder extends (*Macrones aor*).

Apart from those which are characteristic of all Siluroids, no important modifications of the hinder part of the skull are observable in the normal members of the group, either as regards the more

general features of structure or the more special points involved in the mode of formation and relations of the "cavum sinus imparis," or of its bilobed backward prolongation, the "atria sinus imparis." The uniformity in the latter respect is so marked, that a description of those structures as they occur in any one normal Siluroid will practically apply to all the others.

As regards the internal ear, the condition of many of our specimens was such that our observations were necessarily somewhat incomplete. The condition of the membranous labyrinth, and its relations to the cavum sinus imparis and to the atrial cavities, were investigated in a large number of Siluridæ normales but with the purely negative result that we could detect no variations of any importance from the arrangement of these structures, already described for *Amiurus catus* by Ramsay Wright, and for *Silurus glanis* by Weber. In all cases we found a transversely disposed ductus endolymphaticus connecting the two sacculi, and, attached to the ductus, a median pear-shaped sinus endolymphaticus projecting backwards into, and almost completely filling, the "cavum sinus imparis."

With the exception of the intercalarium, the Weberian ossicles exhibit but little variety in shape or in their relations to one another or to the atrial cavities and air-bladder. The variations in the condition of the tripus relate principally to the degree and shape of the curvature of its posterior or crescentic process. In some genera (*Auchenipterus*, *Oxydoras*) the crescentic process is almost straight; in others almost hook-shaped (*Plotosus*); and between these extremes the process may exhibit almost every degree of curvature. A ventral ridge on the root of the crescentic process, to receive the insertion of a slip of fibres from the adjacent anterior wall of the bladder, is very generally present, and varies in size according to the thickness of the walls of the bladder. In some Siluroids (*Macrones*, *Liocasis*) the outer convex margin of the process may be increased for the purpose of fibrous attachment by the addition of an outwardly directed heel-like process. The articular process of the tripus is usually distinct from the complex centrum, with which, however, it articulates at the bottom of a deep pit-like depression. It is very rare, as in one genus (*Auchenipterus*), for the process to be flexible and elastic, and directly continuous by an oblique origin with the anterior part of the neural arch of the complex vertebra like the adjacent and similarly elastic root of the "elastic-spring-apparatus." The proportional lengths of the anterior and crescentic processes vary somewhat in different forms; generally, the two processes are of approximately equal length, but when otherwise it is the anterior which is the longer.

The intercalarium varies greatly in development. Usually a small osseous nodule imbedded in the interossicular ligament, the intercalarium may, in addition, be prolonged therefrom as a horizontal

spicule which terminates in the fibrous wall of the neural canal, between the arch of the complex vertebra and the ascending process of the scaphium, near the dorso-lateral margin of the anterior portion of the complex centrum, with which, however, it is in no way directly attached (*Cryptopterus*, *Callichrous*). In a few genera (*Macrones*, *Liocassis*, *Pseudobagrus*, &c.) the horizontal process is prolonged upwards into a vertically disposed or ascending process, which also lies in the fibrous wall of the neural canal, behind and parallel to the ascending process of the scaphium. In all cases where an ascending process is present it lies between the paired foramina for the exit of the dorsal and ventral roots of the second and third spinal nerves.

The only variations noticed in condition of the scaphium relate to the occasional absence of an ascending process.

Claustra are invariably present, but vary greatly in size, from the condition of extremely slender spicules to somewhat triangular plates (*Pangasius buchanani*).

The air-bladder has the same fundamental structure in all the S. normales. In all cases the organ is more or less cordate in shape, and is subdivided internally by a T-shaped arrangement of a primary transverse septum and a longitudinal septum into three intercommunicating compartments, of which one is anterior and transversely disposed, occupying the anterior third of the bladder, and two posterior or lateral longitudinally arranged chambers, constituting the posterior two-thirds of the bladder. The dorsal wall of the anterior chamber is closely moulded to the ventral and lateral surfaces of the complex and fifth centra, including the subvertebral keel which these centra form, and also to the ventral surfaces of the modified transverse processes of the fourth and fifth vertebræ. The lateral portions of the anterior wall of the chamber are also partially buttressed by the decurved anterior margins of the transverse processes of the fourth vertebra, with or without the aid of the expanded inferior processes of the post-temporals (post-temporal plates), while the median portion of the wall is not infrequently supported by a subvertebral process (*Arius*). The lateral compartments, on the other hand, are neither invested by bone, nor are they in any way directly attached to the skeleton, but lie free in the abdominal cavity. Except in relation to the size of the Fish, the variations in the capacity of the anterior chamber as compared with those of the lateral compartments are but slight, and, as a rule, any increase or diminution in the relative size of the bladder is mainly due to variations in the size of the lateral chambers. With the exception of two genera (*Rita* and *Aspredo*) included in this group, the capacity of the anterior chamber is always much smaller than the combined capacities of the two lateral chambers, and, in one of the two exceptions referred to, the partial suppression of the lateral compartments is compensated by the

development of two large lateral cæca from the anterior chamber. Apart from its partial longitudinal construction into two laterally bulging halves,—a separation which in some cases may be emphasised by the formation of one or two longitudinally arranged and inwardly projecting ridge-like aggregation of fibres from the median line of the posterior, ventral, and anterior walls,—the cavity of the anterior chamber has smooth walls, and is not subdivided by the growth of internal septa.

The lateral compartments may also have undivided cavities (*Auchenaspis*, *Callichrous*, and *Silurus*), but not infrequently they are rendered more inexpansible, and possibly at the same time less compressible, by the formation of a variable number of secondary transverse septa (*e.g.*, *Macrones*), which incompletely subdivide each chamber into a series of transversely arranged, intercommunicating spaces. Occasionally the excessive development of these septa and their union by root-like bundles of fibres, which pass between their opposed surfaces, may lead to the formation of a thick trabecular network of fibrous columns or bands, and to the partial obliteration of the cavities of the two chambers (*Pangasius*).

The width of the primary transverse septum forming the posterior wall of the anterior chamber varies greatly in different Siluroids. In some (*e.g.*, *Auchenaspis*) the septum is co-extensive with the width of the air-bladder, although contracted dorsally to admit of the lateral chambers communicating with the anterior chamber; in others (*Callichrous*, *Cryptopterus*) the septum is reduced to the condition of a narrow, but stout, column-like aggregation of fibres.

Cæcal appendages to the anterior and lateral compartments are not uncommon. The anterior chamber may have small anterior cæca (*Macrones aor*), or much smaller antero-lateral cæca (*Osteogeniosus*). Lateral cæca are sometimes present, and may either take the form of large funnel-shaped structures, which extend the whole length of the abdominal cavity and are entirely free from internal subdivisions (*Rita*), or may occur as small forwardly directed outgrowths, subdivided internally by a network of fibrous bundles, and communicating with the anterior chamber by a number of slit-like orifices in its lateral walls (*Platystoma*). Very rarely (*Callophysis*) are the lateral cæca so numerous as to form a wreath round the lateral regions of the chamber. The lateral compartments are frequently either constricted or prolonged into a posterior cæcal appendage. This may be a longer or shorter tubular, or a slightly oval structure, and confined to the abdominal cavity (*Pangasius buchanani*, *Bagroides melanopterus*), or a long, tapering, tubular structure, which, after traversing the abdomen, extends for some distance along the right side of the tail, between the hæmal arches and the lateral musculature (*Cryptopterus micronema*). In some cases the posterior cæcum is very large, and in

shape an elongated oval body (*Pangasius djambal*, *Malapterurus electricus*), or it may be flattened and leaf-like (*Pangasius macronema*). In one instance (*Oxydoras*) it is very rudimentary. The existence of a pair of rudimentary posterior cæca is very rare (*Auchenipterus obscurus*). Very generally the longitudinal septum extends backwards into the posterior cæcum, and subdivides its cavity into two distinct lateral canals or chambers, which communicate anteriorly with the proper lateral compartments of the bladder. Not infrequently the single or double cavity of the cæcum is partially subdivided internally by a series of circularly disposed, inwardly projecting ridges (*e.g.*, *Malapterurus*). In some Siluroids (*Pangasius*), where the lateral chambers are largely occupied by a trabecular network of fibrous bundles, the cavity of the posterior cæcum is largely obliterated by the formation of a similar growth. It may be remarked that in nearly all the Siluroids with an "elastic-spring-apparatus" that we have examined, posterior cæca were present, although in regard to their size and the extent to which their cavities are subdivided, or partially obliterated, considerable variety exists. In two species only (*Auchenipterus nodosus* and *Pangasius micronema*) are these structures entirely absent.

In all the normal Siluroids, without an exception, a ductus pneumaticus is present and opens into the anterior chamber in the median line of its ventral wall, and immediately in front of the ventral margin of the primary transverse septum.

Not only is the anterior compartment of the air-bladder more or less completely invested by bone on its dorsal and anterior surfaces, but its walls are attached to rigid portions of the axial skeleton and to movable ossicles at certain special points. As to the nature and extent of the fixed skeletal attachments, there is substantial uniformity in the different members of the group, and the physiological effect of such skeletal connexions is, in the great majority of cases, the same, viz., to render the anterior, dorsal, ventral, and posterior walls incapable of participating in any distension of the chamber, which, consequently, must solely depend upon the movements of the lateral walls. The posterior wall, *i.e.*, the primary transverse septum, is always attached by its dorsal margin to the ventral and lateral surfaces of either the complex or the fifth centrum—rarely to the sixth centrum; laterally to this the dorsal edge of the septum is invariably attached to the ventral surfaces of the transverse processes of the fifth vertebra, or to those of the fourth vertebra, or exceptionally to the corresponding processes of the sixth vertebra; and, in addition, a sheet of fibres is generally prolonged forwards, on either side of the complex centrum, into the dorsal wall, where it eventually becomes attached to the radial ridge of its side. We propose to speak of these attachments as forming the "posterior pillars" of the compartment.

As the anterior wall is usually more or less efficiently buttressed by the transverse processes of the fourth vertebra, or by post-temporal plates, or median subvertebral processes, the extent of its attachment to the skeleton varies inversely with the extent to which it is invested or supported by bone. The median portion of the wall is always attached dorsally to the ventral surface and sides of the anterior portion of the complex centrum, often by means of laterally situated, oblique, bony ridges, and also to the radial nodules. Laterally to this, on each side, the anterior wall may be so completely invested by bone as to be free from any special connexion or attachment to rigid portions of the axial skeleton (*e.g.*, *Macrones*); or in correlation with a less complete bony support, the outer stratum of the tunica externa of the anterior wall may separate dorsally from the inner stratum and become firmly inserted into the decurved anterior margin of the transverse process of the fourth vertebra (*e.g.*, *Arius*, *Auchenaspis*, *Pimelodus*). The dorsal attachment of the median portion of the anterior wall to the radial nodules and the complex centrum occurs in all the normal Siluroids, and may be regarded as constituting the "anterior pillars" of the compartment. The ventral wall may also be considered as rigidly attached to the skeleton, both in front and behind, inasmuch as its inner stratum of longitudinally disposed fibres, sometimes thickened into stout inwardly projecting ridges, extends into both the anterior and posterior walls, and shares the skeletal attachments of the anterior and posterior pillars. Although, as a rule, extremely thin, the median portion of the dorsal wall, over an area bounded in front and behind by the anterior and posterior pillars, and laterally by the dorsal walls of the two bulging halves of the chamber, is always firmly attached to the ventral and lateral surfaces of the complex centrum, and possibly also to those of the fifth centrum.

The attachment of the walls of the anterior chamber to moveable ossicles (the tripodes) is effected by the convergence of the fibres of the anterior and lateral walls into the dorsal wall in the form of two triangular sheets, and their ultimate insertion into the crescentic processes of the tripodes, which are situated near the anterior and inner corners of the lateral halves of the anterior chamber. The variations in the extent to which these fibres are attached to the tripodes are mainly confined to one feature. A slip of fibres derived from the median portion of the anterior wall is always inserted dorsally into the ventral ridge of each tripus, or directly into the ventral surface of the ossicle when the ridge fails to be developed. Laterally to this point the fibres forming the whole thickness of the tunica externa of the anterior and lateral walls may converge in the dorsal wall and become attached to the tripodes (*e.g.*, *Macrones*); or as in many other Siluroids (*e.g.*, *Arius*, *Pimelodus*, &c.) the outer stratum of the anterior wall is continuously attached by its dorsal

edge to the transverse process of the fourth vertebra, and only the comparatively thin inner stratum, in addition to the fibres of both strata from the lateral walls, extend into the dorsal walls and constitute the triangular sheets. In the latter case but few, if any, of the fibres of the inner stratum reach the tripodes, which, in consequence, only receive the direct insertion of the outer stratum of the tunica externa of the lateral walls.

Radial fibres arising from the radial nodules and inserted into the concave inner margins of the crescentic processes of the tripodes are invariably differentiated from the dorsal wall of the anterior chamber. In one instance (*Auchenipterus*), where the function of the radial fibres is taken by the flexible and highly elastic articular process of the tripus, the former are but scantily and feebly developed.

As we have previously pointed out, the lateral compartments of the air-bladder are neither invested by bone nor are they directly attached to the skeleton, but project freely into the anterior portion of the abdominal cavity. The most important feature in connexion with their structure, apart from their relatively greater capacity when compared with the anterior chamber, is their separation by a common longitudinal septum and the frequently septate condition of their cavities. Physiologically, the longitudinal septum and the secondary transverse septa subserve the double function of rendering the lateral chambers almost incapable of distension, and at the same time diminishing their susceptibility to the effects of external pressure.

Although we have never been able to detect the presence of intrinsic muscular fibres in the walls of the air-bladder, powerful extrinsic muscles are present in several Siluroids. In *Platystoma tigrinum*, *Pimelodus maculatus*, *P. ornatus*, and *Piramutana piramuta*, a powerful muscle takes origin from the posterior face of the skull, on each side of the foramen magnum, and is inserted into nearly the whole extent of the corresponding half of the ventral surface of the anterior chamber. As the contraction of these muscles must forcibly compress the anterior chamber we shall call them the "compressor muscles" of the air-bladder. They probably occur in many other Pimelodinæ, but, so far as our investigations are concerned, are probably confined to that group.

The presence of compressor muscles is invariably associated with the existence of a pair of much smaller muscles which arise from the exoccipitals, and are inserted into the anterior wall of the anterior chamber of the bladder. The tendon of each muscle has its insertion into the anterior wall immediately external to the complex centrum, and the insertion coincides with the extension of a slip of fibres from the inner surface of the anterior wall to the ventral ridge and concave inner margin of the crescentic process of the tripus. As the contraction of these muscles must evidently have the effect of limiting the

violent excursions of the tripodes which might otherwise take place when the anterior chamber is forcibly compressed by the contraction of its compressor muscles, we would suggest for each the name of "tensor tripodis."

An "elastic-spring-apparatus," provided with powerful protractor muscles, has already been described by Johannes Müller as existing in the South American genera *Auchenipterus*, *Doras*, and *Euanemus*, and in the African Siluroids *Synodontis* and *Malapterurus*. To this list our investigations enable us to add the South American form *Oxydoras brevis*, and the East Indian species *Pangasius buchanani*, *P. djambal*, *P. juaro*, and *P. macronema*. The absence of this mechanism in one species of Pangasius, viz., *P. micronema*, while present in all the remaining species of the genus that came under our notice, is an interesting and noteworthy fact.

In almost all normal Siluroids the lateral or outer walls of the anterior chamber of the air-bladder are more or less extensively and intimately applied to lateral cutaneous areas, and this relation of the two structures is always brought about by the divergence of the dorso-lateral and ventro-lateral muscles of the trunk, combined with the lateral extension of the anterior portion of the bladder.

(II.) *Siluridæ Abnormales.*

Omitting for the present all reference to such extremely aberrant forms as *Hypothalmus*, *Rhinelepis*, and the various Loricaroid Siluridæ, we confine our summary of this group to the various genera and species that have come directly under our notice. These are:—*Clarias*, *Saccobranchus*, *Eutropiichthys*, *Cryptopterus* (two species), *Ailia*, *Schilbichthys*, *Silondia*, *Acrochordonichthys*, *Akysis*, *Pimelodus* (two species), *Bagarius*, *Glyptosternum*, *Amblyceps*, *Cetopsis*, *Callomystax*.

In all these forms the series of rigidly interconnected vertebræ includes only the first, the complex, and the fifth vertebræ, the sixth being almost invariably free. The rigid articulation of the anterior vertebræ to the skull is as marked in this group as in the preceding one, and is brought about by precisely similar means. The centrum of the first vertebra is usually somewhat more rudimentary than in the normal forms, and neither it nor the basioccipital or the complex centrum are ever provided with accessory articular processes. The complex vertebra has the same general characters as in the foregoing group. Radial ridges and nodules are generally but are not invariably present; exceptionally the radial ridge may have no connexion at its inner extremity with the complex centrum (*Clarias*, *Glyptosternum*), and when this is the case the radial nodule may be absent, or confluent with the inner extremity of the radial ridge and widely separated from the complex centrum (*Clarias*).

The most characteristic of the many skeletal modifications which are exhibited in this group is the formation of more or less complete osseous grooves or funnels for the partial or complete enclosure of the air-bladder. Such recesses are formed by the transverse processes of the fourth vertebra, either singly, or in conjunction with those of the fifth vertebra, and vary greatly in depth and in the extent to which they are surrounded by bone. They may be comparatively shallow and widely open on the ventral side, as in *Akysis*, *Bagarius*, and *Glyptosternum;* or may take the form of deep, transversely disposed grooves, contracted distally and somewhat expanded proximally (*Pimelodus sapo*, *Eutropiichthys*, and *Schilbichthys*) ; or they may partake of the nature of transversely arranged bony cylinders or funnels, open distally in the dry skeleton, but otherwise with more or less complete osseous walls (*Clarias*, *Callomystax*, and *Cetopsis*). The transverse processes of the fourth vertebra always form the dorsal and anterior walls of the recesses, and sometimes furnish, in addition, a posterior wall, or even incomplete ventral walls; rarely do they completely enclose tubular recesses (*Cetopsis*) ; more frequently the posterior walls are formed by the transverse process of the fifth vertebra (*Clarias*, *Callomystax*). Exceptionally, a slender, lateral, bony outgrowth from each of the longitudinal ridges bounding the aortic groove in the region of the complex centrum may become attached to the ventral wall of the corresponding lateral air-sac (*Glyptosternum*, *Bagarius*) ; or, as in one instance (*Clarias*), the outgrowths may be strongly developed and form no inconsiderable portion of the ventral walls of the two osseous funnels. Ventrally, the shallow recesses may be closed by a tough fibrous membrane which also invests the corresponding walls of the contained air-sacs (*e.g.*, *Bagarius*); and by the same means vacuities in the walls of the more complete bony funnels are entirely closed (*Clarias*, *Callomystax*). The formation of a horse-shoe-shaped recess by the transverse processes of the fourth and fifth vertebræ in conjunction with plate-like lateral outgrowths from the aortic ridges, which is open laterally and behind in the dry skeleton, occurs only in one genus (*Ailia*). In whatever way the osseous recesses or capsules may be formed they are almost always open laterally or distally in the dry skeleton, and closed by lateral cutaneous areas in the fresh specimen.

The condition of the air-bladder in this group is singularly varied, and in proportion to the bulk of the Fish is always extremely small. Many of its most characteristic features are clearly the results of atrophy and degeneration. The principal modifications appear to be due to the partial or complete suppression of the lateral chambers and the subdivision of the anterior chamber into two laterally situated cavities or air-sacs, either by the solidification of the mesial portion of the bladder or by more or less complete longitudinal constriction.

In all cases the atrophied bladder is partially or completely enclosed within osseous recesses. In one or two instances (*e.g.*, *Schilbichthys* and probably also *Eutropiichthys*) the air-bladder, although solid mesially, nevertheless retains in each half traces of its original and normal division into anterior and lateral compartments, but the extreme thickness of its walls, and the small size of its internal cavities, afford sufficient proof of its degenerate and functionless condition. Solidification of the central portion of the bladder may reduce the cavity of that organ to the condition of a circular canal of fairly uniform calibre, surrounding a massive central pillar (*Silondia*). Two species afford good examples of the extreme variability to which degenerate structures are liable. In one (*Ailia*), the bladder assumes the shape of a tubular horse-shoe, and is almost solid, except at its hollow forwardly curved cornua; in the other (*Pimelodus sapo*) the organ is solid mesially, and of its two pairs of forwardly curved lateral branches one only is hollow and receives the insertion of the tripodes. In one case (*Cryptopterus micropus*, and possibly also *C. hexaptera*) the bladder consists of two partially separated lateral sacs, but its degenerate character is betrayed by the partial obliteration of the cavity of the posterior half by a network of fibrous bundles.

The more frequent condition of the air-bladder in this group is in the form of two simple, pyriform or globose, thin-walled, laterally placed air-sacs, which are either quite distinct or connected by an intermediate tubular portion (*e.g.*, *Glyptosternum*, *Cetopis*, *Acrochordonichthys*, *Bagarius*, *Akysis*, *Clarias*, *Saccobranchus*, and *Pimelodus pulcher*).

The skeletal attachments of the air-bladder both to rigid portions of the skeleton and to movable tripodes exhibit much the same extent and kind of variation as we have already described in the case of the anterior chamber of the more normal Siluroids. In such forms as possess rudiments of lateral chambers and of transverse and longitudinal septa the attachments of the air-bladder to the vertebral column and its processes are quite normal, and even in many members of this group where those structures are entirely wanting, the skeletal attachments are in the main very similar to those of the normal Siluroids. Thus, in those cases in which the air-bladder is represented by two entirely distinct or mesially intercommunicating sacs, the dorsal attachment of the primary transverse septum is represented either by the skeletal attachment of the dorsal edge of the median portion of the posterior wall to the ventral surface and sides of the complex centrum (*Pimelodus pulcher*), or by a similar attachment of the corresponding margin of the posterior wall of each lateral air-sac to the transverse processes of the fourth or fifth vertebra (*Bagarius*, *Glyptosternum*, *Clarias*). The median and tubular portion of the air-bladder, when present, is always thin, and its firm attach-

ment to the ventral surface of the complex centrum evidently corresponds to the skeletally attached medio-dorsal portion of a normal anterior chamber (*e.g.*, *Pimelodus pulcher*). Whether this intermediate tubular portion be present or absent, the inner portion of the anterior wall of each air-sac is always attached to the contiguous lateral surface of the complex centrum, or to the radial nodule, or even to both, after the fashion of the anterior pillars of the normal bladder. Occasionally also, as in such normal forms as *Arius*, the outer stratum of the anterior wall of each air-sac may be dorsally connected with the decurved anterior margin of the transverse process of the fourth vertebra (*e.g.*, *Bagarius*, *Glyptosternum*).

As a rule, where the air-bladder is more completely surrounded by its osseous capsules, the rigid skeletal attachments of the former are not so obvious as in those cases in which the bony investment is but partial.

The relations of each lateral cavity or air-sac to the crescentic process of the tripus imbedded in its dorsal wall are almost precisely the same as in each half of the anterior chamber in a normal Siluroid. The convergence of the fibres composing the anterior, lateral, and dorsal walls of each air-sac, and their insertion into the crescentic process of the tripus, takes place in nearly all the forms included in the present group, but in two or three instances (*e.g.*, *Glyptosternum*) the dorsal wall has partially or completely atrophied, or at all events has so far degenerated that it is extremely improbable that its fibres can possibly exert any pull upon the tripus as the result of any distension of the air-bladder.

Radial fibres are always present, but in some cases are less obviously specialised than in others, and, where radial nodules are absent, pass directly from the lateral surfaces of the complex centrum to the inner or concave margins of the crescentic processes of the tripodes.

Broadly speaking, it may be affirmed that the skeletal attachments of the air-bladder in the Siluridæ abnormales, both to rigid portions of the skeleton and to movable ossicles, are in substantial agreement with those of the anterior chamber of the *S. normales*.

The Weberian ossicles undergo but slight modifications in the different members of this group. Claustra are occasionally absent, and even when present are but feebly developed spicules of bone. As a rule, the scaphium has no ascending process, but only spatulate and condylar processes. The intercalarium may be absent, in which case the interossicular ligament is extremely short, or represented by a very small nodule in the usual position; horizontal and ascending processes are invariably wanting. The tripus is very variously modified. A ventral ridge is rarely present. The crescentic process may be curiously angulated and heeled (*Clarias*); nearly straight with a pointed posterior extremity (*e.g.*, *Bagarius*); or but slightly

curved (*e.g.*, *Glyptosternum*). The articular process is usually long and tapering.

Lateral cutaneous areas are almost invariably well marked and, as a rule, close the distal openings of the osseous recesses in which the air-bladder is lodged, but their relations to the outer walls of the latter vary considerably. In some forms, the structures are in close contact (*e.g.*, *Callomystax*), but more frequently they are separated by a considerable interval which is usually occupied by the lateral lobes of the liver, or by the anterior end of the mesonephros, or even by both.

A ductus pneumaticus may be present or absent. It is usually present where the laterally situated air-sacs are connected by an intermediate tubular portion, but is absent whenever the two air-sacs are completely separated.

The genus *Cetopsis*, referred to above, is one of the genera of Siluridæ in which J. Müller denied the existence of an air-bladder. In a specimen of *C. candira*, however, we found a rudimentary air-bladder in the form of two small oval sacs. Each sac was not more than 6 mm. in length, and was enclosed within the slightly dilated proximal extremity of a tubular or flask-shaped recess, enclosed by the transverse process of the fourth vertebra. The anterior wall of the recess was perforated by a small foramen, near the complex centrum, through which the tripus passed from its attachment to the air-bladder to its connexion anteriorly with the scaphium. As *Cetopsis* is the last of the nine genera of Siluroids in which J. Müller affirmed the absence of an air-bladder about which any doubt remained, it is now not unreasonable to assume that an air-bladder and Weberian ossicles are universally present in the group.

Of the more general conclusions which the foregoing data seem to us to warrant, we shall not now do more than draw attention to the following:—

(I.) The air-bladder and the Weberian mechanism in the Siluridæ are reducible to a common fundamental type, which is perhaps not very dissimilar to that illustrated by the condition of these structures in such normal forms as *Macrones* or *Arius*. From such a type the extraordinary variations met with in different genera, or even in different species of the same genus, are readily derivable, such variations being in part due to increasing specialisation—the result of physiological causes—and partly to the effects of disuse and consequent degeneration.

(II.) The air-bladder exhibits a far higher degree of specialisation in its relation to the Weberian apparatus than in any other Ostariophyseæ, but this fact renders it specially liable to degeneration, when the necessity for the exercise of its special function has,

from any change of habit on the part of the Fish, ceased to exist; and hence the widespread degeneracy of that organ.

(III.) In all the Siluridæ normales the air-bladder is a rudimentary and more or less functionless structure, and the numerous modifications which it presents in this group afford abundant illustrations of the extreme variability to which all degenerate organs are liable.

(IV.) As far as the evidence at our command will enable us to generalise, it seems extremely probable that the degeneracy of the air-bladder in the S. normales is due to their assumption of a ground habit, whereby the continued existence of an air-bladder, capable of functioning as a hydrostatic apparatus, is rendered unnecessary.

(V.) That inasmuch as the assumption of a ground habit is almost invariably attended by degeneration of the air-bladder, which must have the effect of rendering the Weberian apparatus inoperative, it seems to us a reasonable inference that the mechanism in question is related neither to the function of audition as Weber contended, nor to the appreciation of varying atmospheric pressures, as suggested by Sagemehl, but rather to the perception of the varying hydrostatic pressures to which the Fish is continually exposed. (Hasse's theory).

(VI.) Certain facts appear to throw some light on the nature of the Weberian ossicles. The discovery of ascending processes to the intercalaria, which form part of the wall of the neural canal, and are interposed between the foramina for the exit of the second and third special nerves, is confirmatory of the view, first suggested by Baudelot and supported by Ramsay Wright, that the ossicles in question represent the metamorphosed neural arch of the second vertebra. The mode of origin of the tripodes in *Auchenipterus*, if not due to secondary fusion with the arch of the complex vertebra, but to the retention of a primitive continuity, is also confirmatory of the views of the same morphologists, that those ossicles represent the transverse processes of the third vertebra.

VIII. "The Chemistry of the Urine of the Horse." By FRED SMITH, M.R.C.V.S., F.I.C., Army Veterinary Department, Professor, Army Veterinary School, Aldershot. Communicated by Sir WILLIAM AITKEN, F.R.S. Received June 20, 1889.

I have attempted in the following paper to record the results obtained from a series of analyses of the urine of the horse in health.

When I first commenced my subject I was under the impression