

THE SWIM BLADDER OF FISHES A DEGENERATE GLAND.—BY
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On examining, after appropriate dissection, the abdominal viscera of such a fish as a cod or herring, a prominent sac is seen occupying a considerable space underneath the vertebral column or rather underneath the kidneys and dorsal aorta (see Plate 20, fig. 1, *s. b.*). In the herring this sac communicates, as in most physostomous fishes, with the fore-portion of the alimentary canal, really in this case the stomach (Plate 20, fig. 3, *d.*) though as a rule with the œsophagus as in the carp (Plate 20, fig. 2.). The canal may be closed, and in all physoclistous fishes it wholly disappears. The perch (Plate 20, fig. 2), the haddock, (Plate 20, fig. 1), the cod, mackerel, &c., exhibit no duct. In some Teleosteans the swim-bladder is absent and in certain sharks and dog-fishes it is represented merely by a slight diverticulum in the dorsal wall of the gullet. The swim-bladder is, however, of general occurrence amongst osseous fishes, and its primitive character is proved by its mode of origin as a direct pocket or evagination from the pharynx, in the embryonic stages of fishes. The distinguished Scottish anatomist, Professor John Cleland, indeed, expressed the view that the parts of the digestive tract in fishes, so often difficult to determine, may be, in part at any rate, decided by the point at which the swim-bladder is pushed out. (See list of literature referred to, No. 5).

A glance at the extensive and scattered literature, dealing with this interesting organ, shows that very diverse views are

held concerning its nature and meaning. The famous Carl Gegenbaur has referred to the existing uncertainty as to the practical use of this structure (No. 8, p. 566), and one of the most recent contributors to the subject says (No. 24, p. 125) "even now there is much doubt as to the functions of the swim-bladder." From the days of Aristotle its use has been involved in obscurity; but the ancient father of comparative anatomy ventured on the theory that its purpose was to aid in the production of sound, and his successors have again and again revived the theory down to our own day. The Italian, Borelli, regarded it as hydrostatic and an aid to fish in floating (No. 2). A third interpretation is that the organ is respiratory, and in the Ganoids and Dipnoans, it is a complex, vascular, lung-like organ, with an undoubted pulmonary function; but it is by no means certain that the pharyngeal evagination or sac in those highly specialised lung-fishes is homologous with the swim-bladder, and I shall have occasion to point out that exception may be justifiably taken to such a view as that of Dr. A. S. Packard (No. 17, p. 444) who says, "the air-bladder being homologous with the lungs of higher vertebrates, the pneumatic duct is comparable with the trachea of birds and mammals," a view similar to that recently expressed by Professors Jordan and Evermann (No. 11, p. 11) that the swim-bladder is "a sac filled with air lying beneath the backbone of fishes and corresponding to the lungs of higher vertebrates." Professor Arthur Thomson, on the other hand, has given his opinion regarding the view just stated and says (No. 23, p. 397), "that the lungs and air-bladder are homologous is by no means certain; but the comparison is plausible." A further view interprets the swim-bladder as a barometer. Sagemahl (No. 21) regarded it as such, so that like an aneroid instrument, it informs the fish of changes in the atmospheric pressure affecting the surrounding water. Minor modifications of these views have been broached by other authorities; but a full examination of the facts seems to lend little support to any of them.

It is important at this point to notice the nature of the gaseous contents of the swim-bladder, so far as these have been ascertained. Most of the older authorities declared that it was filled with air, although Provençal and Humboldt, nearly a hundred years ago (it was in 1809), published an analysis which showed that, in some cases, oxygen filled the sac, while in other examples only 1% to 5% of the contents consisted of oxygen, and the greater portion was nitrogen. They thought that the oxygen increased with the depth of the fish's habitat, a view which later investigations have proved to be erroneous. In the fishes, for instance, brought up from the greatest depths of the sea, during the cruise of H. M. S. "Challenger," very little oxygen was found in the swim-bladder, while in specimens frequenting the surface waters that gas formed quite a considerable percentage. (No. 4, Vol. I, p. 226). Fish from a depth of 2875 fathoms showed not more than 4% to 5% of oxygen in the swim-bladder, but, at the surface, specimens of fish were found to have 34% or 35% of oxygen in the gaseous contents of the organ. Configliacchio and Biot discovered a large proportion of oxygen in specimens from fairly deep water, and the most recent authority on the subject (Professor R. W. Tower, of Brown University, U. S. A.), states that at a depth of from 35 to 70 fathoms the walls of the swim-bladder secrete oxygen very actively. The organ has nervous branches, gastric filaments, from the Vagus nerve, as well as a sympathetic supply, and, according to Bohr's experiments, division of the tenth nerve stops all secretion of gas, while section of the sympathetic nerve hastens the secretion of gas. Dr. Günther (No. 9, p. 142) has stated that, in fresh-water species, little oxygen gas as a rule is found, nitrogen prevailing, with just a trace of carbonic acid; but in sea-fishes the amount of oxygen is much larger. In a fresh-run salmon Dr. John Davy found 10% of oxygen, a trace of carbonic acid, and nearly 90% of nitrogen, an observation of a remarkable nature as the fish had only just left the sea, probably. All observations tend to show that there is no

foundation for an idea somewhat prevalent, that air or gas is forced from the gullet of the fish through the pneumatic duct into the swim-bladder. In those fish without a duct (Physoclisti) that is impossible, and in them as well as in Physostomes, the gas is evidently secreted by the vascular walls, the *retia mirabilia* of the organ. The varying proportions of the gaseous elements named, seem to show that no very important function is subserved by them. Nitrogen, which in the animal organism is excreted largely as urinary and faecal waste, has been found to be absorbed under two peculiar conditions, viz.: when an animal is in a state of inanition, and when an animal changes its food and is accustoming its system to new forms of nutriment, a fact of singular interest, to which further allusion will be made on a subsequent page. The secretion, on the one hand, of oxygen or, on the other hand, of nitrogen may depend upon the special chemical conditions prevailing in the water being breathed by fish. Of the purely chemical causes which control the appearance and movements of fishes, one of the principal has been found to be the abundance or scarcity of oxygen mingled with the sea water. The absence of herrings from the Arctic seas has been frequently commented upon. The minute crustacean life which is so attractive, and so essential, it may be added, to the vast schools of herring, is extremely rich in the cold northern waters, yet herring do not appear to resort to those regions, whereas on both sides of the Atlantic the waters, adjacent to this continent and to the British Islands and the European continent, abound with herring. The Atlantic is more richly oxygenated than the Arctic seas, and this comparative lack of oxygen is no doubt the main factor in deterring the herring from migrating thither. Experiment has clearly demonstrated the dependence upon temperature of the absorptive power of sea water. Barometric pressure too is important in determining the amount of atmospheric air absorbed, and as this air loses its oxygen far more rapidly than its nitrogen in its descending passage to deeper strata of water, these deeper

strata are of necessity imperfectly oxygenated, and unless disturbed by moving currents, unable to support the higher forms of animal life. As was shown by observations in the Swedish fisheries, the presence or absence of the usual schools of certain fish was almost solely influenced by the greater or less amount of water rich in oxygen pouring into the Baltic Sea from the open ocean. Active migratory fishes, such as mackerel and herring, must be largely controlled by these conditions, especially in waters more or less inclosed or separated from the open oceanic areas.

The line of thought here opened up is one of great practical as well as scientific importance; but I have treated elsewhere* of this and cognate matters affecting the environment of fishes and need not say more in this place. Nitrogen, as compared with oxygen, is of inferior moment in the vital processes, especially the respiratory processes, of the animal frame; but the amount of oxygen present in the swim-bladder, especially in fishes whose circumstances would seem to demand an ample supply, is too insignificant in quantity to be important in the oxidation phenomena going on in those organisms. The nature of the gases, which occupy the chamber of the swim-bladder would, indeed, seem to be wholly unimportant physiologically and dependent upon contingent circumstances. Fishes without a swim-bladder have, at any rate, no corresponding storage of gases.

The object of this paper is to show how little support prevailing theories (as to a hydrostatic, respiratory, barometric, accoustic, or other function) receive from the facts, and that whatever adaptations the swim-bladder may undergo, it is clearly not primarily in function either hydrostatic, accoustic, or sound-producing, respiratory, barometric, or for balancing or floating purposes simply. I would point out in the first place this most remarkable fact that, without exception, the anatomists who have treated of the functions of this organ, have ignored

*No. 18. p. xlviii.

all reference to its special features in the embryonic or larval stages of fishes. To understand the true nature and significance of any organ it is necessary to study its development, yet no authority, so far as I am aware, has made reference to the remarkable features of the swim-bladder in the embryonic stages. Few have had the opportunity to study the larval development of fishes possessing this organ; and my own researches show, as might have been expected, how in the larval stages the swim-bladder reveals its primitive character, and that the variations in its form, position, connections, and minute structure, observed in adult fishes, are secondary, non-essential, and very seriously misleading. It is, however, on these secondary and misleading modifications that authorities have, almost without exception, based their views as to the nature and meaning of the swim-bladder in fishes. On very flimsy and inadequate evidence many eminent authorities have not hesitated to attribute extremely varied functions to this organ, and it is certainly remarkable that the most generally adopted views have the least support from observation. Young larval fishes in the sea swim in a reversed position, back downwards, and it might be supposed that the development of the swim-bladder aided them in "righting" themselves, and progressing dorsum uppermost, as they do later in life; but those without the organ adopt the latter position as readily at the accustomed stage as those possessing it. If it be hydrostatic it is difficult to see why fish specially needing buoyancy, like the surface frequenting sharks, the ponderous oceanic sunfishes (*Molidæ*), often more than a ton in weight*, the huge tunny, the mackerel, &c., should be destitute of it, while the shore-loving *Gobiidæ*, *Scorpænidæ*, *Triglidæ*, *Gastrosteidæ*, &c., have it well developed and of large size. The *Sciænidæ*, including no fish frequenting the deep waters of the open sea, have this organ in its most elaborate forms. It is large in the fresh-water whitefishes

*This monstrous fish (*Mola*) as Packard says, (No. 17, p. 462), "is like others of the order, a surface swimmer."

(*Coregoni*), the grayling (*Thymallus*), the shallow-water Gastrosteidæ and the river-ascending salmon, none of which seem to need any such supposed potent help to give them floating power. On the other hand, in the sea bass it is small, and in all the Serranidæ it is adherent to the abdominal walls. No fishes apparently need this organ less than the fresh-water suckers, yet without exception the Moxostomidæ and Catastomidæ, grovelling on the bottom of rivers and lakes, have a swim-bladder, consisting of two or three large sacs. To fish like the cod and certain deep-water lake whitefishes, it appears not only useless to aid them in rising in the water; but may even be fatal to them for when brought up from the bottom the expanded swim-bladder may seriously disorganize the fish and force the abdominal viscera out of the mouth. The halibut and flat-fishes can rise in the water, though these fish, so much in need of such an instrument of buoyancy, are not provided with it: neither are the Scombridæ (with such exceptions as *Scomber japonicus* as already pointed out) although to quote Mr. Boulenger (No. 1, p. 65) this family are "unceasingly active, their power of endurance in swimming being equal to the rapidity of their motions." The Cottidæ or Gurnard family have a well-developed swim-bladder yet, as the authority just quoted says, they are "bad swimmers and generally living at the bottom near the coasts" (No. 1, p. 62) —just as the Polynemidæ have a large swim-bladder, yet are purely littoral fishes, frequently hovering about the estuaries of rivers. The immortal Baron Cuvier, struck by the erratic occurrence of this supposed buoyant provision, admitted that he saw no meaning in it and was unable to understand the want of so large an organ, not only in fishes which frequent the bottom, like skates and flat-fishes, but in many others which apparently, he said, were second to none in their rapidity and their facility of movement, such as the mackerel.

Its position immediately behind the cephalic or branchial section of the alimentary tract and its communication by an

open duct with the gullet, in almost all embryo fishes and in so many adult forms, with the frequent presence of a blood-vascular network, naturally suggested a respiratory use. It is not surprising that a respiratory function has been very commonly attributed to it. Many fishes are known to swallow air at times. The stone-loach (*Cobitis*) habitually passes air through its richly-vascular alimentary canal, as does the West Indian *Callichthys*. After oxygenating the blood circulating in the walls of the stomach and intestines, it escapes in bubbles posteriorly. The sea-raven (*Hemitripterus*) also distends its stomach with air, while carp and similar fish, in foul or muddy water, swallow air in quantities. Professor Alexander Agassiz pointed out that *Lepidosteus* when $\frac{3}{4}$ inch long, during the second or third week after hatching, rises to the surface of the water to swallow air, as it continues to do in adult life. Wilder observed the same habit in the bow-fin (*Amia*) of the Great Lakes, a regular exhalation and inhalation of air, after the manner of salamanders and tadpoles, which come to the surface of the water for air with increasing frequency as the larval branchiæ shrink and disappear. In certain Teleosteans, such as the Labyrinthici, where this resort to respiration by means of the walls of the alimentary tract might be readily anticipated, there is instead a special organ, which develops in an accessory branchiæ cavity (Plate 23, fig. 7). Strangely enough, when these fish such as *Ophiocephalus* and *Anabas* are no longer in the water and are compelled to breathe air, the (closed) swim-bladder is not even then utilised; but the vascular laminae of the supra-branchial cavity are relied upon. Again, the Globe-fishes (*Gymnodontes*), which have the habit of distending their bodies by inflation so that the spines, studding their integument, project on all sides as a formidable armour, do not use the swim-bladder as one would expect; but either "inflate a sub-oesophageal sac (which has a muscular sphincter, and extends beneath the skin of the abdomen) rendering themselves balloon-like," as Professor Macalister says (No. 14, p. 85), or fill the

stomach, or in other cases, the distensible gullet, with air for the same end. It is possible that these fishes having swallowed air for purposes of respiration, the habit has been turned to this other (defensive) purpose; but the important point to note is this that the swim-bladder has been utilised in these fishes neither for respiration, nor for defensive inflation and flotation. It is reasonable to suppose that in the assumption of a post-branchial respiratory habit the œsophagus would be utilised. That is the view of all anatomists; but, if an organ, so frequently present as the swim-bladder, be really respiratory, there must in addition to this very exceptional and abnormal habit among fishes of swallowing air, be developed an appropriate blood-circulation, *i. e.* venous or impure blood must be conveyed to the sac for the purpose of purification (oxygenation); but this is an arrangement not existing in any fishes excepting Ganoids and Dipnoi.

The features presented by the blood supply lend no support to the "respiratory" theory. The essential feature of respiration is the conveyance of impure or venous blood to a special organ for purification (oxygenation)*, the oxygenated blood passing away to the body, and leaving the carbonic acid to be got rid of in the readiest way; but the swim-bladder totally differs from such an arrangement. It is in fact supplied with arterial blood almost direct from the aorta or aortic arch. In such a form as the haddock (*Melanogrammus aeglefinus*) the two epibranchial arteries unite, it is needless to say, to form the dorsal aorta, and on each side anterior to the union is given off a sub-clavian artery to the pectoral fins, and in front of the sub-clavian on the right side are given off two visceral arteries (the coeliac and the mesenteric) the latter going to the swim-bladder, but in the sharks it goes to the spleen, pancreas and intestine. From the swim-bladder the blood goes into the

*As Claus (Lehrb. d. Zool.) says "The blood must necessarily absorb oxygen and exhale carbonic acid. This interchange of gases effected between the blood and the medium in which the animal lives is the essential feature in respiration either in the atmosphere or in the water."

hepatic portal system. The oxygen which may fill, or nearly fill the swim-bladder cannot be regarded as destined for the purpose of charging with oxygen, or arterialising, the blood, for that is already arterial, and has just been charged with oxygen in the gills. Günther states (No. 9, p. 142) that the oxygen is really secreted by the surface of the swim-bladder, and there is every reason to hold that view; but such a process is therefore secretory, not respiratory in the accepted sense. Again, it must be noted that in such a fish as the haddock (Plate 20, fig. 1. *sb*) with a swim-bladder having extremely vascular walls, and a rich blood-supply, the organ is closed and the contained gas cannot pass out by a duct, whereas in the carp (Plate 20, fig. 4) with vascular fanlike tufts, in the pike (*Esox*) with small compact red bodies in which arterial and venous capillaries anastomose and in the sturgeon, salmon, herring, &c., though unprovided with these *retia mirabilia*, the swim-bladder is not closed, but has in most cases a very capacious opening through the dorsal wall of the œsophagus. The fact, on which Professor Rolleston laid stress (No. 19, p. 424), that in all species, when the branchiæ are in full activity, the swim-bladder is supplied with the purest arterial blood, lends little support to the supposition that it, in any way, subserves respiration. Of course in Dipnoans, like *Lepidosiren* and *Ceratodus*, the pulmonary function is undoubted; but the fact that the duct is ventral and not dorsal as in the Teleostei is of the highest importance. What is there to make improbable the suggestion that these so-called lungs are new structures correlated to the change in the circulation and the more highly differentiated condition of the heart. Wilder, it is true, states that in *Amia* and *Lepidosteus* he has found cases intermediate between the dorsal and ventral connection of the swim-bladder; but even if this variation of the duct be regarded as not wholly exceptional and abnormal, it cannot account for a dorsally-placed organ like the swim-bladder becoming a ventrally-placed lung, nor that a pulmonary artery, really a branch of the inferior aortic arch, carrying venous blood, should

supplant the mesenteric artery which supplies the organ in most fishes and that the blood leaving the swim-bladder should go direct to the heart rather than to the portal vein. In *Ceratodus* (a case of exceptional significance) the *arteria coeliaca* supplies the swim-bladder, and the duct of the swim-bladder exhibits a glottis.* True lungs, we know, arise as paired buds from the ventral surface of the cesophagus (Plate 21, fig. 3), and it is questionable to regard them as homologous with a dorsal diverticulum such as the swim-bladder of fishes (Plate 21, figs. 1 and 2). They may be, and probably are, structures arising *de novo*. May not this also be true of the lung of the Dipnoan fishes, as the swim-bladder and its connecting duct may disappear, and have done so completely in many fishes?

Closely connected with the supposed pulmonary character of the swim-bladder is the theory that it is an aid in sound-production. A hollow vesicle filled with gas may act as a resonator. We know that in certain fishes sounds are produced. Thus, as Dr. C. C. Abbott pointed out, the mud sunfish (*Acantharchus pomotis*) makes a grunting sound, the gizzard shad (*Dorosoma cepedianum*) a whirring sound: the chub-sucker (*Erimyzon sucetta*) utters a prolonged note due, it is said, to the air forcibly driven through the duct of the swim-bladder, the cat-fish (*Ameiurus*) hums softly, the "Drums," like *Aplodinotus grunniens*, make a grunting or croaking noise, and such species of the Sciaenidæ, as *Pogonias* make a loud drumming sound, especially loud in the male fish, while the eel (*Anguilla*) is declared to utter a musical note of a distinctly metallic character. These sounds, says Dr. S. A. Packard, are homologous with those of reptiles, birds, and mammals, being produced by the swim-bladder, which that authority holds to be the homologue of the lungs. Dr. W. R. Hamilton (9 a, p. 63) made however some experiments on the croaking of the fresh-water drum-fish, which is provided with

*Since this paper was written I find that Professor Albrecht of Brussels laid stress on the ventral connection of lungs and the dorsal position of the swim-bladder and its duct, and strongly opposed the homology of the swim-bladder and lungs.

large pharyngeal teeth. "While moving its grinders as I supposed the fish had done during life," said Dr. Hamilton, ". . . an exact imitation of the croaking of the perch was produced. I produced the sounds in a similar manner within the hearing of several Alleghany River raftsmen and Ohio River fishermen at intervals during the day on which I experimented, without allowing them to know how the noises were made, or that a perch was used for the purpose and they all declared it was an exact imitation of the croaking of the perch. . . . I cannot conceive of any way by which the sound could be produced by the air-bladder of the fish, as its physiological functions and anatomical structure do not indicate its use as a vocal organ." Dufosse (No. 7) attributed to the extrinsic muscles vibrations which produced sounds aided by the resonance of the swim-bladder; but in other cases he attributed the sound simply to gas violently driven through the pneumatic duct of the organ. The late Professor J. A. Ryder combatted this view which had been urged to account for the noise produced by *Aplodinotus*: "the usual view that the air is forced from one part of the air-bladder to another in the Sciaenoids seems to me inadequate in the absence of clearly worked out demonstrations. The group is physoclistous, or has the air-bladder entirely closed" (see note on p. 63, No. 9 a). Sorensen (No. 22) regards the organ as a resounding device, and thinks that it would have disappeared had it not so functioned. Yet the fact remains that most fishes are silent, and fish such as the cod and carp have never been credited with any gifts of voice, notwithstanding the size and high development in these fishes of the swim-bladder. The vastly greater number of fishes, which possess the swim-bladder, more or less highly developed, produce no sounds. They are silent and the organ occupying so large a space in the super-abdominal space is unutilised for that purpose. It is also remarkable in the extreme that some of the most active and buoyant fishes should be without this organ (*e. g.* the sharks and the family Scombridæ, or Mackerels, for

the most part). It is difficult to see why trout, carps, pike, sticklebacks, and sturgeon, frequenting shallows, where a hydrostatic organ is comparatively useless and unnecessary, are provided with it, while the Sand-launce (*Ammodytes*), the lump-fish (*Cyclopterus*), or the mackerel, should be without it. Its erratic occurrence shows how unessential it is to fishes now, however important it may primitively have been.

It is in the early condition, as seen in the embryonic and larval stages of fishes possessing this organ, that the swim-bladder is most interesting and suggestive. It has all the features characteristic of a large but simple gland. Krause distinguishes (No. 12, p. 206) four parts in a simple gland (1) the mouth, (2) the neck, (3) the body, (4) the coecal extremity, and these may all be noted in the early swim-bladder, which is really a blind sac provided with a duct, and usually having an abundant blood-supply. Glands are always well supplied with blood, as their function is to secrete some characteristic substance from the blood passing through their vascular net-work. The swim-bladder arises, in all cases, as a dorsal bud or pocket of cells on the upper wall of the hind portion of the oesophagus. (Plate 1, figs. 21 and 2). At the earlier stages the gullet cannot be clearly marked off from the mesenteron or stomach. Thus, in a haddock, a few days before hatching, an evagination from the dorsal side of the alimentary canal is observed projecting perpendicularly from the centre of the gullet. (Plate 21, fig. 4 *sb*). In the same microscopic section shown in the plate, a ventral diverticulum also appears, viz., the rudiment of the liver (*l*). The section was in a slightly oblique transverse vertical plane, and therefore includes both organs. The lengthening of the alimentary canal, owing to the rapid growth of the young fish, soon more widely separates the swim-bladder and the liver, and, it may be pointed out, causes the straight canal to twist or curve to one (the left) side, and the balloon-shaped bladder curves over to the right, (Plate 21, fig. 5, *sb*). For some days

after hatching, the organ retains its simple cellular character, a single layer of large endodermal cells, not distinguishable from the cells forming the wall of the general alimentary tract. Soon a layer of flattened mesoderm cells (Plate 21, fig. 5, *mes*) creeps round and invests the organ, becoming later the connective tissue layer or tunica externa. The mesoderm cells rapidly become greatly thickened, as the larva grows, and the lining endoderm cells assume a swollen glandular character. Thus in *Trigla*, the gurnard, when $\frac{1}{4}$ in. (6 mm.) long, the cells are so enlarged as to crowd against each other, producing a very irregular internal lining, forming thick rugæ, the nuclei of the cells being, moreover, distally situated near the free ends of the cells, the contents of the cells being clear and non-staining (Plate 21, fig. 6). In a Gadoid, of the same length (6 mm.), probably a pollack or coal fish, a similar appearance is presented; but the nucleus of each swollen cell is central not distally excentric in position and the fine fibrous layer outside, really very much flattened and attenuated mesoderm cells, shows dense black pigment (Plate 21, fig. 7, *p.*) The presence of massed pigment cells, forming a dark patch in the region of the swim-bladder, is a marked feature in certain young gadoids (Plate 21, fig. 11).

In sections of a young Gadoid $\frac{1}{8}$ inch (6.5 mm.) long, probably a young cod or pollack I cannot now say which, for these allied species are practically identical in internal structure in larval life, the pigment layer is now more distinctly separated, and the nuclei in the large clear cells lining the swim-bladder are proximal and nearer to the thickened connective tissue layer. (Plate 21, fig. 8). In slightly older post-larval Gadoids say $\frac{3}{8}$ inch (9.2 mm.) long the cavity of the swim-bladder has greatly increased, the large mucus cells, with proximal nuclei are more regularly arranged (Plate 21, fig. 9), but a posterior portion of the organ is now marked off, with thin walls and showing no mucus-cell lining, indeed a dense thickened tubular section separates the anterior and posterior parts, in the wall of which

an artery now appears, while the two urinary ducts or ureters pass down each side of the swim-bladder posteriorly to the urinary vesicle behind. In a young *Callionymus* $\frac{1}{3}$ inch (7.8 mm.) long, the swim-bladder is capacious, and its walls thin, and membranous; but the floor is thick and its lining cells form dense rugæ not showing the clear mucoid character generally distinguishing the internal cells of the organ in many species. (Plate 21, fig. 10). The herring (*Clupea harengus*) of the same size, but no doubt very much older than Gobioids or Gadoids such as those just described, exhibits a very capacious thin-walled swim-bladder, the epithelial layer of cells being reduced in thickness. The larva was $\frac{1}{4}$ inch long (about 7 mm.) and the notochord was extremely large, while the alimentary canal was a narrow tube of very small capacity. Sections of a Gurnard (*Trigla*) $\frac{5}{8}$ in. (10 mm.) long, proved most interesting as the walls show no less than five distinct layers and an anterior portion with the usual mucus cell-lining was succeeded further back by a blastema of deeply stained tissue in which clear cells, possibly blood form-elements, are massed. Each rounded clear cell showed a definite deep-stained nucleus. This appearance suggests that a high vascularity is already characteristic of the interior of the swim-bladder at this early stage. The capacious front portion still, however, retains the glandular features, the large clear lining cells, each with a proximal nucleus, resting upon a dense nucleated stratum, outside being a complexly massed fibrous layer, external to which is a fourth stratum of flattened cells, three or four cells deep, the nuclei very marked, but much flattened, and outside all is a thick connective tissue layer (the tunica externa) composed of long interlaced fibres. Thus in the front part of the organ there are no less than five layers, (Plate 21, fig. 12, *a. b. c. d. e.*); but in the second portion the large-celled epithelium ceases, and the four outside layers described are present. The pigmented peritoneal membrane which encloses the organs of the abdominal cavity appears below the swim-bladder anteriorly; but further

back it ceases, and the organ lies directly upon the liver and alimentary canal. The peritoneum never indeed surrounds the swim-bladder, at any time during the life of the fish. If an embryologist, or an anatomist, were for the first time confronted with an organ having the characteristics of the swim-bladder in fishes during their early larval life, he would, without hesitation, pronounce it a gland. The salivary glands, for instance, in the human subject develop in the six-week embryo as a protrusion of the deeper epithelial layer of the mucous coat of the oral cavity becoming hollow after its protrusion and developing follicles, in which occur large transparent cells, each with an excentric nucleus stained by carmine while the surrounding mass of cell-substance remains clear and unstained. Other cells, called "peripheric," occur in the follicles which are not mucous, but albuminous and stain completely. Dr. W. B. Carpenter said (No. 3, p. 132), "It is believed that the albuminous cells during the period of rest of the gland gradually become metamorphosed and develop into the mucin-holding cells." I do not wish to attach too much importance to the circumstance; but in one specimen of a cod, $11\frac{1}{2}$ mm. ($\frac{1}{4}$ inch) long, the anterior portion of the swim-bladder was lined, not by large clear cells, with a nucleus alone staining by carmine; but a dense deep staining mass of reduced agglomerated cells as though the large cells had become metamorphosed into something like the small dark granular cells which fill the salivary acinus during the period of active secretion. The swim-bladder, in its earliest condition, may be compared to a large gland, not compound and complexly developed like the liver; but a simple sac or huge follicle, its fundus or distal region lined by large epithelial cells, and leading into a non-glandular second portion, which may indeed be regarded as having subserved a storage function like the gall-bladder in that great secreting gland, the liver, and finally leading by a duct to the opening into the gullet which may or may not have a sphincter muscle. This duct may in a large number of species

of fish wholly degenerate later. In the pike-perch or pickerel (*Stizostedion vitreum*) exhibiting when adult a ductless swim-bladder, still possesses the duct when the fish is 6 or 8 inches long, and it is even then hollow for a great part of its length. In the familiar stickleback (*Gastrosteus*) the duct persists and remains open for a comparatively long time, although in the adult stage it disappears.

I have made reference to the salivary glands in speaking of the glandular character suggested by the early features of of the swim-bladder. Fishes exhibit no salivary structures whatever, unless the lingual follicles in the Lamprey be of that nature; but if, as I think it is clear, or at any rate not improbable, that the swim-bladder was primitively a gland, which has lost the glandular function, then its function cannot have been remotely unlike a secreting organ, active in providing a medium for lubricating food in the anterior portion of the alimentary canal. Such lubrication of the food became of course unnecessary in fishes, such as the Sharks which practically possess no oesophagus for the huge stomach opens directly to the mouth and the food is gulped at once into that capacious digestive chamber, the mouth with its array of teeth and the wide gullet have chiefly the task of preventing the escape of the seized prey. There are many glands in Vertebrates now without use or whose use is difficult to understand yet they persist. The small finger-like pocket in the rectum of Sharks (the rectal gland) is not understood. In the Chimaeræ or Rabbit-fishes, closely allied to the sharks, it has degenerated, and forms merely a slight projection on the intestinal wall. A still more remarkable case is the thyroid gland in man, the origin of which must be sought not in the fishes, but in the still lower and more primitive Urochordata or Tunicates. The hypobranchial groove or endostyle of the Ascidiæ, whose cellular ridge, on the internal ventral wall of the pharynx, secretes a mucus which entangling the particles of food, is passed, by the dorsal lamina, to the digestive tract. The

endostyle has an alimentary function and is found in the Enteropneusta (*Balanoglossus*). It is represented in the larval lamprey, and in *Amphioxus*, and, indeed, in some stages, in all Craniota. As the tongue, in the higher forms, becomes more important and grows, the endostyle is reduced and assumes the character of a canal closed off from the mouth cavity. It persists as the thyroid gland in the highest Vertebrates, indeed in man himself, but its original physiological relations and purposes are lost, and it becomes wholly disconnected with the digestive canal. As Dr. T. M. Studler (No. 20) has shown the right thyroid rudiment, in a $5\frac{1}{2}$ weeks embryos (*Homo*), is still connected with the pharynx; but its fellow on the left is further advanced and has lost its primitive connection.*

The swim-bladder is an outgrowth of the stomodaeum or rather the posterior buccal portion of the alimentary canal, the part which in a great majority of animals is very well provided with glands. If it be, as I have ventured to suggest, a degenerate gland, its anterior position is explained, much as its connection may shift later in obedience to physiological and anatomical exigencies, ceasing, indeed, to have any oesophageal connection whatever in the physoclistous fishes. In such a fish as the herring, it does not communicate with the pharynx, but with the gizzard-like crop, while its posterior attenuated continuation opens by a duct on the left side of the anus (Plate I, fig. 3, *x*.) Its persistence in so many fishes, though it has disappeared in so many, may be explained by its deep position. An organ removed from the external modifying conditions, which may not merely reduce but obliterate useless organs comparatively rapidly, do not affect so potently a deeply-seated useless organ and the tendency is for such an organ not to disappear but to be modified for a variety of functions. It is easy to understand, therefore, not only its persistence, but its actual increase in size and complexity in spite of its increasingly unimportant and

*Other glands might be referred to, such as the thymus which is largest in man two years after birth and diminishes with age, while the thyroid, which is largest at birth, may wholly disappear in the adult.

non-essential character. Its form and relations may become most surprising in character. Its minute structure may show the most perplexing variation. The delicate membrane which forms the silvery tubular sac in the herring (*Clupea*) Plate 20, fig. 3, *sb.*, or the capacious ovate organ attached to the inner surface of the dorso-lateral body-wall in *Perca*, Plate 20, fig. 3, *sb.*, is in great contrast to the thick massive-walled swim-bladder of the sturgeon (*Sturio*) (Plate 23, figs. 1, and 2), or the spongy, complexly meshed and vascular organ seen in the Bowfin (*Amia calva*). Special muscles occur in the walls. They are usually striped *i. e.* voluntary, and under the control of the fish; but the duct possesses unstriped muscle, excepting in the rare cases where a sphincter muscle is present for closing and opening the entrance to the duct. Humboldt thought that the muscles of the swim-bladder effected its compression, and aided in the descent or ascent of fishes in the water, an idea which M. Delaroche (No. 6) admitted, might be possible though his own researches rather pointed, not to effecting by the swim-bladder such a change in the specific gravity of the fish as compared with the surrounding water, but rather to keeping it at the same specific gravity as the watery environment and presenting the fish rising or sinking. M. Morcau, in his later researches (No. 16) confirms Delaroche's view and adds that the equilibration is due to the external pressure of the water upon the body walls, and he emphatically contradicts Humboldt's idea and asserts that the muscles on the walls of the swim-bladder are not used to regulate or alter the volume of that organ.

In general the walls of the swim-bladder exhibit four layers in the adult fish viz.: (1) a ciliated lining epithelium; (2) an inner fibrous layer, often silvery in appearance, due to wavy fibres or to bright crystalline rods; (3) an outer thick fibrous layer, yielding isinglass, and especially dense in *Sturio*; (4) a very delicate muscular stratum, which may be so arranged as, it is claimed, to compress and drive the

contents of the posterior chamber into the anterior chamber of the swim-bladder. The internal vascular structures are very simple and confined to one portion of the swim-bladder as in the conger, (Plate 22, fig. 1), which exhibits two red rounded vascular bodies (*a.a.*) situated near to the entrance of the pneumatic duct, or the blood-vascular network is spread over a large portion of the internal surface forming, as in the haddock, a dense reticulum of blood-vessels, or again these *retia mirabilia* may be wholly absent. In size the swim-bladder varies exceedingly, it may be small as in many of the herring family but simple in form, (Plate 20, fig. 3, *sb.*) It may as in the common perch (*Perca flavescens*) be still simple but of larger capacity as compared with the size of the fish, (Plate 20, fig. 2, *sb.*) Thus in a 10 inch perch the swim-bladder is no less than 4 inches long and nearly an inch in diameter, while in a perch $7\frac{1}{2}$ inches long the organ is 3 inches in length. Its volume is not more variable than its shape and relations to other organs in the fish possessing it. In very young post-larval fishes it forms a prominent feature, glistening like a silvery gaseous bubble of elongated shape through the translucent body (see figure of Cunner $\frac{1}{2}$ inch long, Plate 21, fig. 13, and Plate 23, figs. 3, 4, 5, 6.) Instead of the simple ovate sac of the Perch and Cunner, it may become extremely elongated as in the Herring sending forward a pair of delicate ducts, which end in two swollen sacs in the skull, close to the ear, one on each side, or as in the Haddock or Cod ceasing all connection with the alimentary canal, the capacious sac may continue forwards as two solid vermiform cornua terminating near the ears, (Plate 20, fig. 1, *corn.*) In the Carp the pneumatic duct not only persists but the anterior sac of the two-chambered swim-bladder may directly connect with the vestibular sac of the ear by ligaments and a chain of three bones, (Plate 20, fig. 4, *i. k. l.*), really costal modifications, the last and longest being attached to the swim-bladder, (*sb.*) In the Siluroids the relations of the two organs are far more complex, for the anterior vertebræ may coalesce

and their lateral processes expand as a roof or bony shield over the anterior portion of the swim-bladder. Even the South American species *Hypophthalmus*, so universally regarded by anatomists as lacking the swim-bladder, has been proved by Professor Ramsay Wright to be no exception, the rudimentary swim-bladder being present, completely paired (really two separated vesicles), and partly enclosed in the vertebral body and the walls of the neural canals and in the ossified *tunica externa* (No. 26, p. 116), while it has connection with the auditory organ by a chain of ossicles much reduced, but as Dr. Wright points out, "after precisely the same plan as in the other Siluroids," (loc. cit. p. 108). On each side a so-called malleus connects with a stapes, by an incus, with the lateral wall of the atrium sinûs imparis, the bones named being modified portions respectively of the first, third and second vertebræ. The stone-loach (*Cobitis*) like its congeners generally (the Acanthopsidæ) exhibits a bony case on each side of the most anterior vertebræ, in which the two globular chambers of the swim-bladder are enclosed side by side.* The two protecting bullæ are expansions of the transverse processes of the second and third vertebræ, (Plate 20, fig. 5, *bb.*), and hide from view the chain of three ossicles. The tropical American and African Characinidæ have a swim-bladder divided into two parts connecting by a chain of ossicles, with the auditory organs as in the Carps and Siluroids. The Cyprinodonts, diminutive carp-like fishes very abundant in Canada, have, however, no such auditory connection by a series of ossicles, while one Central American species, *Rivulus*, has been found to be destitute of the swim-bladder altogether. The carps (*Cyprinidæ*) and the pikes (*Esocidæ*), and other families like the oceanic Halisauridae, possess a simple swim-bladder, often a two-chambered sac with thin membranous walls, opening into the gullet by a tube, while

*The swim-bladder in *Heterobranchus* and *Malapterurus* exhibits the two rounded sacs. (Plate IV, figs. 8, 9.)

in the physoclistous perches, of which *Perca flavescens* is a familiar example, and in the Squamipinnes (the brilliantly tinted chaetodonts, &c.), it is likewise simple in form and structure often showing a trace of anterior bifidity, (Plate 20, fig. 2). It may still preserve its simple sac-like form, but be paired as in *Gymnotus*, the electric eel, or completely bifurcate as in the physoclistous Brotulidæ and Acanthuridæ. In the simple swim-bladder of the cod or haddock, (Plate 20, fig. 1.), a number of lateral processes fringe the upper margin of the organ on each side, corresponding with intervertebral spaces, while a pair of cylindrical solid prolongations pass forward to the auditory region; but in the Sciaenidæ, excepting *Larimus*, which has a simple sac, the fringe of lateral processes becomes elaborate. In *Pogonias*, the Drum-fish, they are broad, leaf-like, and laterally unite on each side in a tube which opens into the posterior end of the organ, (Plate 22, fig. 4.). In *Johnius* they form a complicated fringe of ramose pectinate processes and in the example of a Sciaenid swim-bladder figured by Dr. Günther over a hundred of these pectinate, much subdivided, processes occur, (Plate 22, fig. 3.). Another type of swim-bladder is represented in this family by such a form as that assumed in *Corvina*, (Plate 22, fig. 2.) There seems, indeed, to be no limit to the variation in the details of this organ in various groups. The internal cellular or sacculated character found in the swim-bladder of the *Notopteridæ* seems to presage the elaborate lung-like structure in some Ganoids and in the Dipnoans; but I have stated the grounds for not regarding this latter organ as the homologue of the swim-bladder. It may be, and for the reasons set forth in this paper I do not doubt that it is the case, that the ventral air-bladder or subœsophageal sac even in Teleosteans such as the Gymnodonta, extending beneath the skin of the abdomen and opening by a duct, with a sphincter muscle, into the gullet, is a new structure and not homologous with the dorsally connected swim-bladder of Teleostei generally. If the modern sharks have lost the swim-bladder, or show

merely a rudimentary trace of it in some species, and if so many Teleosteans have become bereft of this organ and now show no traces of ever having possessed it, I see no improbability in the view I now urge that the Ganoids and Dipnoans, possessing a ventrally-placed lung-like sac, have acquired it as a new development, a new organ, and that it, not the dorsally connected swim-bladder of other fishes, is the prototype and homologue of the lungs of higher Vertebrates. This organ, arising *de novo* as it seems to me, was provided with a vascular supply (a venous connection) quite different from that, an essentially arterial one, which is exhibited by the swim-bladder in most fishes.

Regarding, then, the swim-bladder as primitively a gland whose original use is gone, like so many disused organs in the animal frame, can it be said that it has any use now, or have the various functions attributed to it, hydrostatic, acoustic, barometric, respiratory, &c., little or no basis in fact? I have already pointed out that nitrogen has been found by physiologists associated in the living organism with a state of dormancy and inanition, and with altered alimentation, *i. e.*, a change in the nature of the food. Both these states are characteristic features in the life of fishes. Whether fish sleep or not is a matter of controversy; but that they may pass into a state of dormancy, a condition of inanition, is well-known, while the changes in the diet of fishes, at various ages in the young, and at particular seasons in the adult fish, are recognized by all authorities. The storage of nitrogen, secreted from the blood circulating in the vascular network of the swim-bladder, may be associated with either or both of these states, a state of dormancy or inanition, or a state induced by a marked change in the character of the nutriment or food consumed. In venturing to interpret the swim-bladder as a glandular structure, whose original function has gone, I have done so because that interpretation best accords with its character in the embryonic and larval condition of the fishes possessing it. To all the

other various interpretations which have been put forth, serious, and to my mind, fatal objections exist.

In conclusion I may sum up the points on which I would lay emphasis. The swim-bladder, in its earliest condition in the embryo and the post-larval stages, exhibits the characteristic features of a secreting gland, opening by a duct into the anterior portion of the alimentary canal. It arises as a protrusion from the digestive tract like the hepatic evagination which becomes the liver, but this huge gland (the liver) with its capacious bile-duct is on the ventral side whereas the swim-bladder is on the dorsal side of the tract. The degeneration and disappearance of the swim-bladder in so many fishes proves that it is clearly not essential for flotation. Some of the most active pelagic species like the Sharks, Sun-fishes, Mackerels and others are without it, while fishes like the Pleuronectidæ and other bottom-frequenting species likewise lack that organ, though apparently so much in need of a hydrostatic device to facilitate their ascent or descent in the water. Inshore littoral fishes and shallow-water species (freshwater and marine) are almost without exception provided with it, though so little needed, in their case, for floating purposes. If its hydrostatic utility be questionable, it is clearly not for respiratory purposes, as in most fishes venous blood is not conveyed to it; but blood which has immediately before been arterialisèd and fully purified in the gills. Its dorsal connection and position superior to the alimentary canal indicates that it is not the homologue of the pulmonary organs with their duct opening on the lower side of the œsophagus. Professor Arthur Thomson pertinently observes, (No. 23, p. 391), "The air-bladder lies dorsally and is almost always single: the lungs lie ventrally, and are double, though connected by the gullet by a single tube. It is not certain that these outgrowths are homologous, though the air-bladder of Dipnoi acquires the functions of a lung." That the swim-bladder aids in audition, and in sound-production or voice, is suggested by the chain of ossicles (the complex Weberian apparatus) in such fishes as the

Siluroids, and Carps; but it has never been demonstrated by experiment that these fishes have hearing or sound-producing powers superior to other fishes not possessed of this apparatus. The sturgeon and cod, though provided with a large swim-bladder are silent. If the swim-bladder, again, be barometric why is it denied to so many fishes to which a knowledge is necessary of the variations in pressure of their atmospheric and aqueous surroundings? The presence of the organ in different families of fishes, as Gegenbaur points out, indicates some important purpose, though it may be said that the persistence of numerous obsolete and disused organs is most remarkable, the thymus gland being a familiar example. An external or exposed organ, which becomes useless may disappear rapidly like the pectoral fin of the lower side in the variegated sole (*Solea variegata*, Donov.), but an internal deep-seated structure is more likely to remain and become modified rather than disappear. Such transformation and change of function the swim-bladder of fishes has unquestionably undergone.

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LIST OF REFERENCE LETTERS IN THE PLATES.

<i>a.</i>	anus		mes. flattened mesoderm cells clothing the swim-bladder.
<i>bl.</i>	gall-bladder.		
<i>b. b.</i>	bony expansions of vertebral processes.	<i>oes.</i>	oesophagus.
		<i>ov.</i>	ovary.
<i>corn.</i>	cornua or anterior processes of swim-bladder.	<i>pigt.</i>	pigment.
		<i>pyl.</i>	pyloric caeca.
<i>d.</i>	duct of swim-bladder.	<i>pyl. o.</i>	pyloric opening in stomach.
<i>do.</i>	opening of do do in oesophagus.	<i>sb.</i>	swim-bladder.
<i>epith.</i>	large epithelial cells lining developing swim-bladder.	<i>spl.</i>	spleen.
		<i>stom.</i>	stomach.
<i>go.</i>	genital opening.	<i>sup. c.</i>	superior occipital bone of skull.
<i>ht.</i>	heart.	<i>vert.</i>	vertebrae.
<i>l. k. l.</i>	chain of ossicles from ear to swim-bladder.	<i>x.</i>	orifice of swim-bladder near anus in <i>Clupea</i> .
<i>int.</i>	intestine.	<i>y.</i>	opening of pneumatic duct in swim-bladder.
<i>k.</i>	kidney.		
<i>l.</i>	liver.		

DESCRIPTION OF PLATES.

Plate 20.

- Fig. 1. Haddock (*Melanogrammus aeglefinus*, Linn.) dissected to show the ductless swim-bladder *in situ*.
- Fig. 2. Perch (*Perca flavescens*, Mitch.) dissected to show the ductless swim-bladder with slightly bifid anterior end.
- Fig. 3. Herring (*Clupea harengus*, Linn) dissected to show the swim-bladder with anterior process, the duct (d) opening into the stomach, and the posterior opening (x) on the left of the anus (a).

- Fig. 4. German carp (*Cyprinus carpio*, Linn.). The swim-bladder (s b) connected by duct (d) with the œsophagus (œs) and with the ear by a chain of ossicles (i. k. l.). (Modified from Weber's well-known figure).
- Fig. 5. Ventral view of skull and anterior vertebræ of the loach (*Cobitis barbatus*, Linn.), showing osseous bullæ which cover the swim-bladder. The bullæ are expansions of the lateral processes of the 2nd. and 3rd. vertebræ.

Plate 21.

- Fig. 1. Diagram, showing the diverticulum or rudiment of the swim-bladder on the dorsal wall of the œsophagus of an embryo fish, viewed from above.
- Fig. 2. The same, viewed laterally.
- Fig. 3. Diagram, showing the bifid diverticulum or rudiment of the lungs on the ventral wall of the œsophagus of a frog. Viewed from below. (Modified from Wiedersheim).
- Fig. 4. Section (trans. vert.) of the œsophagus of an embryo haddock (*Melanogrammus*) inside the egg, three days before hatching, showing dorsal diverticulum or swim-bladder (s b.) and ventral diverticulum or liver (l). The section was cut in a somewhat oblique vertical plane.
- Fig. 5. Section (trans. vert.) of larval haddock, three days after hatching showing more advanced condition of swim-bladder, liver, gall-bladder, and covering of flattened mesoderm cells. x 200.
- Fig. 6. Section (trans. vert.) of portion of swim-bladder of gurnard (*Trigla gurnardus*) 6 mm. long. x 175.
- Fig. 7. Section do. do. of cod (*Gadus morrhua*) 6 mm. long. x 175.
- Fig. 8. Section do. do. of pollack (*Pollachius virens*) 6.5 mm. long. x 200.
- Fig. 9. Section do. do. of cod, 9.2 mm. long. x 200.
- Fig. 10. Section do. do. of gemmous skulpin (*Callionymus lyra*) 7.8 mm. long. x 200.
- Fig. 11. Forepart of larval haddock (from life), 7 days old, showing the swim-bladder (sb.) above the stomach (stom) and densely covered with black pigment.
- Fig. 12. Section of portion of swim-bladder of gurnard (10 mm. long) showing five distinct layers in the walls.
- Fig. 13. Post-larval cunner (*Tautoglabrus adspersus*, Walb.) showing swim-bladder (s b) in transparent body of the fish. x 8.

Plate 22.

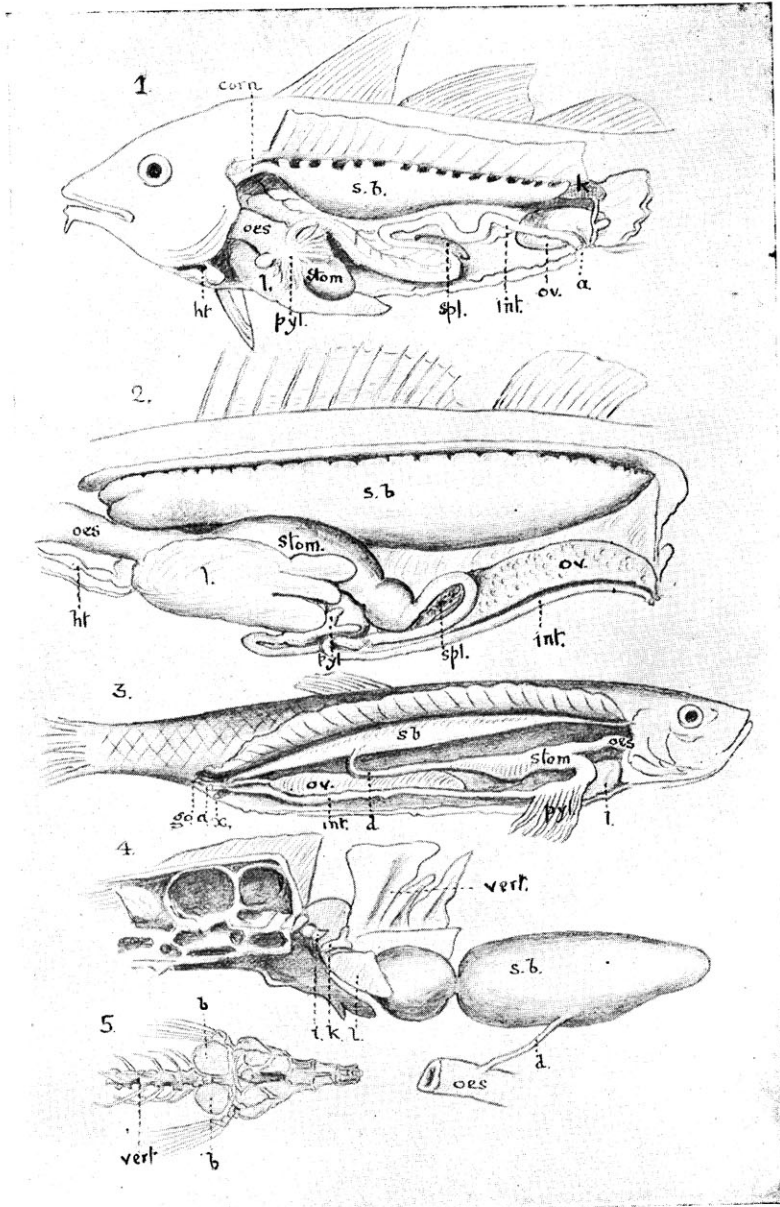
- Fig. 1. Dissection of stomach, swim-bladder, &c., of the conger (*Conger vulgaris*, Cuv.) showing two globular vascular bodies (a. a.) near the opening of the duct in the swim-bladder (s b.)

- Fig. 2. Swim-bladder of *Corvina* (after Cuvier and Valenciennes).
 Fig. 3. " " " a Sciænoïd (after Günther).
 Fig. 4. " " " *Pogonias chromis* (after Günther).

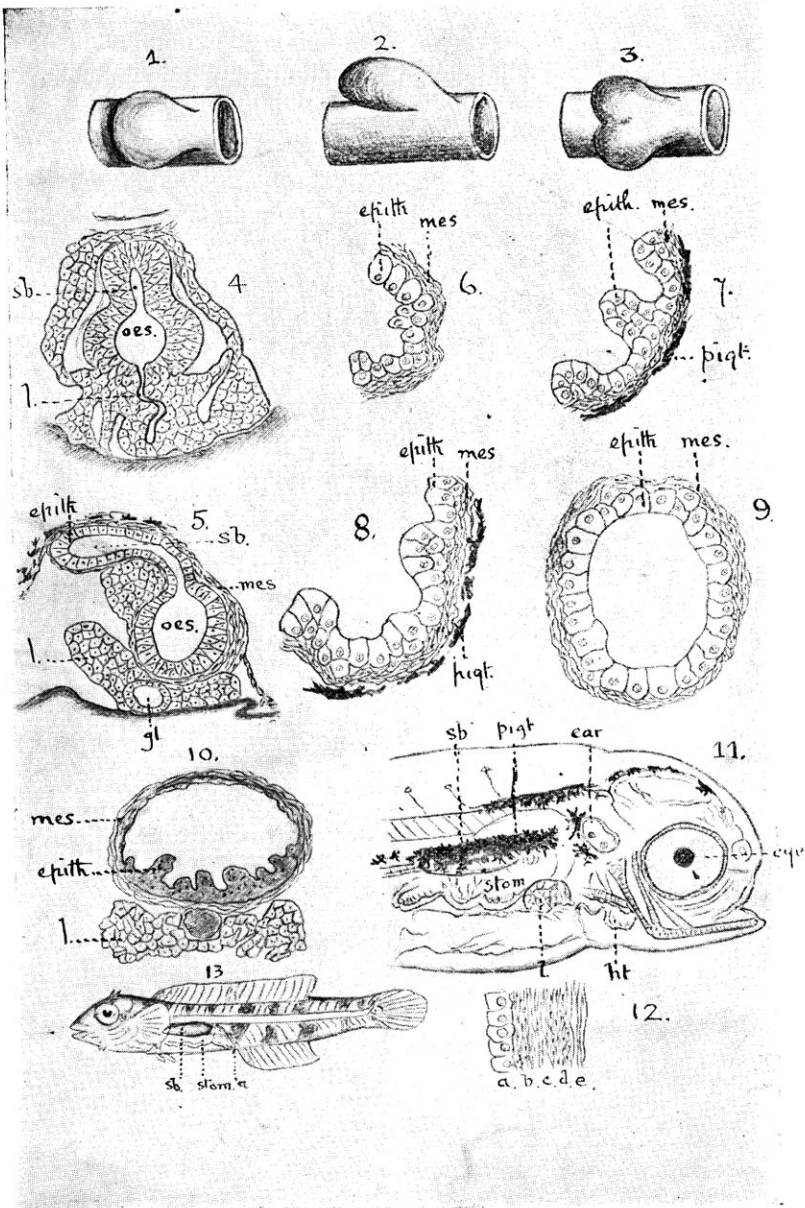
Plate 23.*

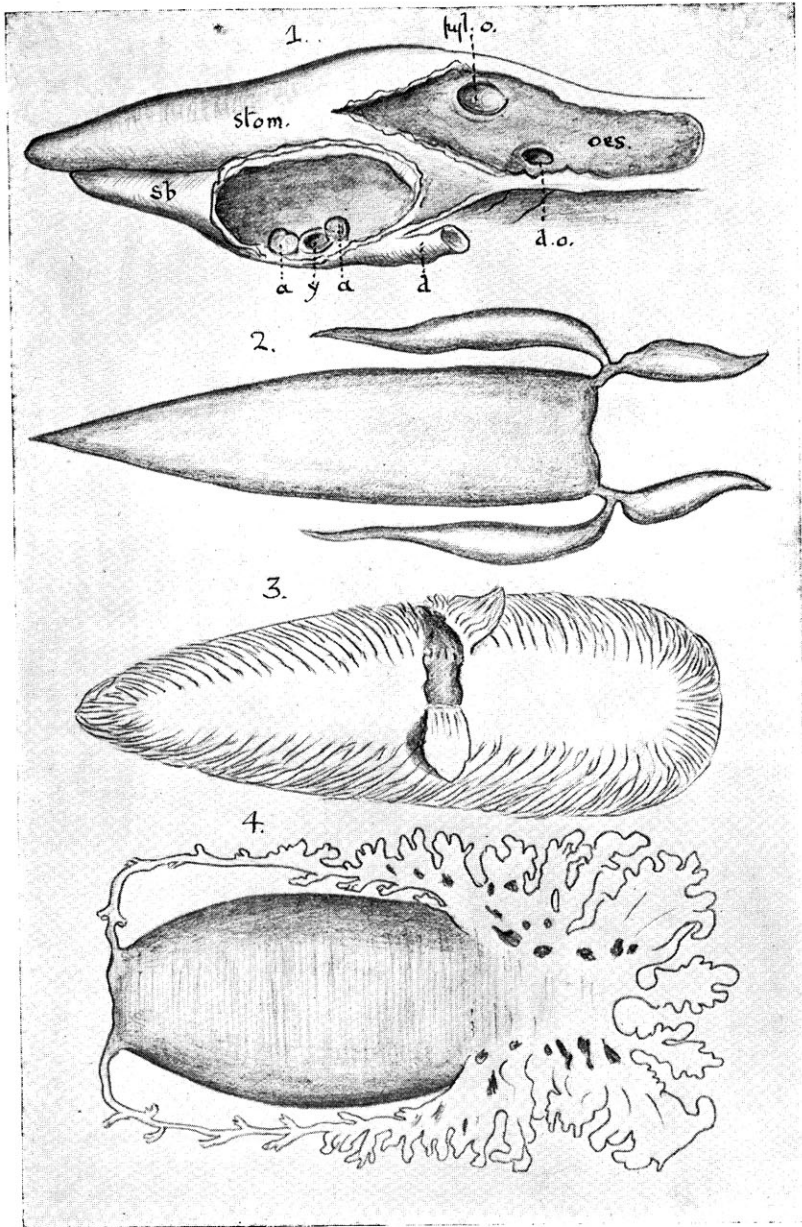
- Fig. 1. Abdominal viscera of young sturgeon viewed from above, showing capacious swim-bladder (s b.)
 Fig. 2. The same showing upper side of swim-bladder (s b.) cut away to show the interior with opening of pneumatic duct (y.) and radiating fibres.
 Fig. 3. Newly hatched gaspereau (*Pomolobus pseudharengus*, Wilson) showing large swim-bladder (s b.) and anterior cornu (*corn.*) x 20.
 Fig. 4. Post-larval smelt (*Osmerus*) 15. 5 mm. long. x 7.
 Fig. 5. Post-larval Thwaite-shad (*Clupea finta*) 20 mm. long, showing small elongated swim-bladder (s b.) x 5.
 Fig. 6. Post-larval goby (*Gobius*) 11 mm. long with conspicuous ovoid closed swim-bladder (s b.) x 10.
 Fig. 7. Head of climbing perch of India (*Anabas scandens*) showing supra-branchial organ above the gill-chamber proper.
 Fig. 8. Swim-bladder (s b.) of *Heterobranchus* divided into two globular sacs.
 Fig. 9. Swim-bladder of *Malapterurus* showing a third chamber posterior to two incomplete rounded sacs, outer tunic partly lifted away and exposing second layer.

*Figs. 1 and 2 after J. A. Ryder (Bulletin U. S. Fish Comm. Vol. VIII, 1888.); 4 and 5 after Ernst Ehrenbaum, (Wissenschaft. Meeresuntersuch., Erster Band Hef., Beitr. 3. Naturgeschichte einig). Elbfische, 1894); 6 after E. W. L. Holt (Sci. Trans. Roy. Dub. Soc. Vol. IV. 1891); and 8 and 9 after Redouté in Histoire Naturelle (Égypt): Poissons, by Geoffroy St. Hilaire.



Face b. 226.





Face p. 226.

