THE AIR OR SWIMMING BLADDER OF FISHES.

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EVERY fisherman is familiar with some of the forms of the organ known as the air-bladder found in many kinds of fish, whether tenants of our ponds and rivers or of the sea. Sometimes he may remember being startled to hear a gurgling sound proceed from the trout from whose mouth he is extricating the fly: this sound is occasioned by the air being forcibly pressed by the hand out of the air-bladder through the œsophageal orifice. The subject of the swim-bladder of fishes is one of considerable interest to the naturalist; let us take a short survey of it.

The organ in question is found in most osseous fishes*; it extends along the back of the abdomen, between the kidneys and the intestinal canal. The forms of this air-reservoir are various. Sometimes, as in the perch, it is a simple elongated cylinder closed at both ends; sometimes, as in the carp, tench, roach, and other *Cyprinidæ*, the organ is divided crosswise into two portions, by a deep constriction with a minute orifice leading from the one portion to the other; or these two compartments may have no communication with each other, as in *Bagrus filamentosus* and a species of *Gymnotus*. Sometimes, as in the genera *Arius*, *Polypterus*, and *Lepidosiren*, this organ is divided lengthwise into two compartments; or it may be bifurcate; or divided into "four longitudinally succeeding portions," as in the genus *Pangasius*, one of the *Siluridæ*. The sapphirine gurnard (*Trigla trirundo*) has a swim-bladder divided longitudinally into three lobes, of which the middle one is the largest; in other gurnards it is bilobed. "Sometimes the air-bladder is divided partially, both lengthwise and crosswise, as in *Cobitis fossilis*, *Auchenipterus furcatus*, and some species of *Pimelodus*." In *Corvina hispinosa* the air-bladder gives out two somewhat slender processes on each side, one extending upwards, the other in a contrary direction. The

* It is also found in the Cartilaginous Sturgeon.

maigre (*Scicena aquila*) presents an air-bladder with a fringe all around its edge, which consists of numerous ramified pneumatic cæca. In *Gadus Navavaga*, Professor Owen tells us, "the lateral productions expand and line corresponding expansions or excavations of the abdominal parapophyses, thus foreshadowing the pneumatic bones of birds. In *Kurtus* the air-bladder is encircled by expanded ribs, curving and meeting below it." In Amia the air-bladder exhibits such a cellular structure that Cuvier could compare it to nothing else than the lung of a reptile; this cellular subdivision is still more strikingly shown in the Lepidosiren or mud-fish. Thus we have, as it were, a complete series of modifications, from the simple elongated cylinder of the perch or herring, through the various forms exhibiting cæcal processes, up to the completed lung-like structure of the air-bladder of the Lepidosiren. The air-bladder consists of two membranes, an external tendinous membrane of a silvery colour, and an internal mucous membrane lined with flat or "plaster epithelium," and supplied with blood-vessels which either divide into fine branches, in a fan-like form, or else form what have been termed *retia mirabilia* at particular points. These *retia mirabilia*, or vaso-ganglions, may readily be seen in the air-bladder of an eel, in the form of red glandular-like bodies of an oval shape. In some fishes a duct leads from the air-bladder to the stomach or the œsophagus: this is known by the name of the *ductus pneumaticus*. It is a simple membranous tube, presenting, however, much diversity in length and diameter, and also in its point of communication with the digestive apparatus. "In the herring the *ductus pneumaticus* is produced from the posterior attenuated end of the cardiac division of the stomach, and opens into the fusiform air-bladder at the junction of the middle and posterior thirds of that organ. The long narrow and flexuous *ductus pneumaticus* is continued from the fore part of the posterior division of the air-bladder in the Cyprinoids, and opens into the dorsal part of the œsophagus; the short, straight, and wide ductus pneumaticus in the Lepidosteus opens also into the dorsal part of the œsophagus, the orifice being served by a sphincter. In the *Erythrinus* the air-duct communicates with the side of the œsophagus; in *Polypterus*, as in *Lepidosiren*, with the under or ventral part of the beginning of the œsophagus." * The contents of the air-bladder of fishes have been analysed by Humboldt, Biot, and others, and, strange to say, remarkable differences are stated to exist, according as the fish are fresh-water or marine. The air consists of a mixture of nitrogen and oxygen, with traces of carbonic acid gas: in fresh-water fishes the largest

* "Comparative Anatomy and Physiology of Vertebrates," vol. i.

percentage of nitrogen occurs; in salt-water fishes oxygen is said to occur in the largest proportion. Some, I believe, have maintained that the air of the swim-bladder of carps consists of pure nitrogen. Humboldt, who experimented on the electric eel (*Gymnotus electricus*), found the gas of its air-bladder to consist of 96° of nitrogen and 4° of oxygen. Biot, on the other hand, experimenting on some deep-sea Mediterranean fishes, discovered 87° of oxygen, the rest nitrogen, with a trace of carbonic acid. This, if an undoubted fact, is certainly a singular anomaly, and I confess I share, with the late Dr. Davy, some doubt as to the accuracy of the experiments. "That the same organ should secrete two gases so very different in their nature, appears anomalous, and deserving of further enquiry. Indeed, does not the entire subject need more minute enquiry? At present the facts relating to it are few, and seem far from adequate to allow of very satisfactory conclusions being drawn as to the use of the bladder and its secretion in the animal economy; except of a mechanical kind, as effecting the specific gravity of the fish. Were the gas uniformly of one kind, were it constantly azote, it might be easy to assign it a plausible end, the function of the air-bladder might be inferred to be auxiliary to that of the kidneys. The secretion of oxygen is the anomalous fact, so contrary is it to the ordinary course of changes in living animals, in which the general tendency is to the consumption of oxygen—*à priori*, one might almost as much expect oxygen to be exhaled from the lungs, in respiration, as to be separated from the blood by secretion by the air-bladder; and had we not the authority of so accurate an observer as M. Biot, we might be led to suspect that the statement of its being so was founded on error." †

How does the air gain admittance to the air-bladder? In the case of those fish whose air-bladders possess no ductus pneumaticus, it is clear that the gas must be secreted by the inner membrane of the bladder from the blood; but in fishes which are provided with a ductus pneumaticus, so as to lead to a communication with the œsophagus, the air may in a great measure be derived from the atmosphere, as in the case of trout when they rise at a fly. This opinion was held by Rathke and Dr. Davy. Further experiments on this interesting subject are very desirable, for we seem to know at present very little positively about it. We have seen how varied is the form of the air-bladder in those fishes which possess one; let us now notice its presence or absence in the different orders. In the *Cirrostomi* and *Cyclostomi*, represented by the British lancelot (*Branchiostoma*) and lamprey (*Petromyzon*) respectively, the

† "Physiological Researches," p. 271.

air-bladder is entirely absent; in the *Malacopteri* we meet with fish possessing both a swim-bladder and an air-duct (*ductus pneumaticus*); the *Anacanthini* exhibit in several instances an air-bladder, but no ductus pneumaticus; in the *Acanthopteri* we meet with an air-bladder but no duct; the same is the case with the *Plectognathi* and the *Lophobranchii*; the *Ganoidei* show, in some of the genera of the order, an approximation to a lung-like structure of the air-bladder, which is often cellular and provided with an air-duct. The *Holocephali* have no swim-bladder, neither have the *Plagiostomi*. The *Protopteri*, to which the Lepidosiren belongs, possess a double air-bladder, very cellular and lung-like, with air-duct, glottis, and pulmonary vein.

With regard, however, to the existence of this organ in the different orders, it must be borne in mind that it is occasionally absent in fishes belonging to different genera, and sometimes even in fishes exhibiting merely specific differences. We are thus, naturally enough, driven to the question of *cui bono*? what are the functions of the swim-bladder and air-duct when present? Are they such important organs as by some people they are said to be? What does their presence indicate, and will it serve to throw a gleam of light on that most interesting of all riddles, the origin of species? Paley considers that "the air-bladder of a fish affords a plain and direct instance not only of contrivance, but strictly of that species of contrivance which we denominate mechanical. It is a philosophical apparatus in the body of the animal." This philosophical apparatus is thus described by Roget in one of the "Bridgewater Treatises:" "Independently of these instruments of progression (tail and fins), most fishes are provided with internal means of changing their situation in the water.

"The structure by which this effect is accomplished is one of the most remarkable instances that is met with of an express contrivance for a specific purpose, and of the employment of an agency of a class different from that of the mechanical powers usually resorted to for effecting the same object. When distended with air it renders the whole fish specifically lighter than the surrounding water; and the fish is thus buoyed up and remains at the surface without an effort of its own. On compressing the bladder by the action of the surrounding muscles the included air is compressed, the specific gravity of the whole body is increased, and the fish sinks to the bottom. On relaxing the same muscles the air recovers its former dimension, and the fish is again rendered buoyant. Can there be any stronger evidence than the placing of this hydrostatic apparatus, acting upon philosophical principles, in the interior of the organi-

sation for a purpose so definite and unequivocal?" * Cuvier says, the "most obvious use of the swim-bladder is to keep the animal in equilibrium with the water, or to increase or reduce its relative weight, and thereby cause it to ascend or sink in proportion as that organ is dilated or compressed. For this purpose the fish contracts the ribs or allows them to expand. Certain we are, that when the air-bladder is burst, the animal remains at the bottom, turns up the belly, and becomes deficient in the powers of motion. A curious phenomenon is observed in fishes caught with hook and line at great depths and drawn up suddenly; for the air contained in their swim-bladder expands, as they are ascending, more rapidly than they can counteract by compression, and either it bursts and the abdomen becomes inflated, or by expanding forces the œsophagus and stomach out at the mouth." Cuvier maintained that there is no sufficient foundation for assuming that the swim-bladder offers any analogy to lungs. Professor Rymer Jones, in speaking of this organ, remarks—"In connection with the locomotive organs we must here notice one of the most elegant contrivances met with in the whole range of animated nature, by which the generality of fishes are enabled to ascend towards the surface or to sink to any required depth without exertion." The general function of the swim-bladder, there can be little doubt, is a mechanical one; nevertheless, it does not seem to me that this organ is of such importance, and such an elegant contrivance, as has been so repeatedly affirmed. For how is it, we may fairly ask, that in different genera of fishes of precisely similar habits, some have an air-bladder, others have not? We can understand why it should be absent in the *Pleuronectidæ*, whose habits confine them to the bottom of the water, or in the angler with similar habits; but when we find that one surface-swimming mackerel has a swim-bladder and another species of precisely similar habits is devoid of one, it is obvious, notwithstanding the general function of the organ when present, that it is by no means an essential adjunct to swimming. Of the two sun-fish (*Orthagoriscus*) which occur in our own seas, one has a swim-bladder, the other none at all. Many of the *Siluridæ* possess a large and sometimes complex swim-bladder, but genera occur in which there is no swim-bladder at all. So, again, fish that, for the most part, keep to the bottom are devoid of this organ; but in the mud-loving eel we meet with swim-bladder and pneumatic duct. Experiments, too, if I am not mistaken, have been made according to which, after the puncture of the bladder and the severing of the muscles which act upon it, and even after its complete removal, the fishes have

* "Animal and Vegetable Physiology," vol. i. page 429.

been able to rise to the surface or descend with perfect ease.* According to Professor Kner the form and size of the swim-bladder, its position and development of vesicular glands, not only differ in the various genera and species, but, curiously enough, they vary in one and the same species of fishes of the family *Murænidæ*. Professor Owen has some interesting remarks on the absence of the air-bladder in the surface-swimming sharks:—"Though the air-bladder serves it also enslaves. It opposes, for example, those fishes that possess it in their endeavours to turn on one side, and it demands a constant action of the balancing fins to prevent that complete upsetting of the body which it occasions from the weight of the superimposed vertebral column and muscles when life and action are extinct. The sharks require, by the position of their mouth and in their common pursuit of living prey, freedom in turning and great variety as well as power of locomotion; if they are not aided by a swim-bladder, neither are their muscular actions impeded by one; whilst their swimming organs require that degree of development and force which suffices for all the evolutions they are called upon to perform." But it would appear that there are exceptions to the general rule of the absence of a swim-bladder amongst the *Selachians* (sharks and rays), for, according to the investigations of Micklucho-Maclay, certain selachians are possessed of a rudimentary air-bladder: is this rudimentary organ the remnant, as it were, of a swim-bladder that once existed in a fully developed form in selachians of some remote age, or must we regard it as a new and independent growth? On this question a few remarks will be made by-and-by. Undoubtedly, the most interesting point for consideration is that one which relates to the question whether or not the swim-bladder of fishes is the homologue of the lungs of air-breathing vertebrates. Functionally in all fish, with, I believe, the exception of the *Protopteri*—represented by the two species of Lepidosiren, one belonging to the American, the other to the African fauna—the air-bladder has no relationship with a lung. Its function is generally a mechanical one, of no great importance, however, and occasionally, as in the carp, it serves to intensify sounds in relation to the sense of hearing.

There can, however, be no doubt that, "under all its diversities of structure and function, the homology of the swim-bladder with the lungs is clearly traceable." True, there is nothing at all in the simple cylindrical, closed air-bladder of a perch to remind one of the cellular structure of the lung of an

* Since the above was written I have found that the experiments are recorded in the "Annales des Sciences Naturelles" for 1866. The paper (Du rôle de la Vessie natatoire) is by M. Édouard Gouriet, and is very interesting.

Amphibian, but, as we have seen, there are numerous gradations, leading by various transitions from a single cavity up to a highly complex cellular organ, which both in structure and function is indisputably a lung. The fishes which most closely resemble the amphibians belong to the orders *Ganoidei* and *Protopteri*. Now, in the first of these orders we find a swim-bladder, often cellular, as well as an air-duct. The curious bony pikes of S. America (*Lepidosteus*), remarkable for the hard bone-like scales with which they are covered, and the allied genus *Polypterus* of some of the African rivers, belong to this order. Lepidosteus has an undivided air-bladder with a wide pneumatic duct; Polypterus possesses a double air-bladder and a pneumatic duct communicating with the œsophagus. If we turn to the *Protopteri*, we shall find in the Lepidosiren the transitions completed, for here we find a double lung-like air-bladder with air-duct, glottis, and pulmonary vein—and this respiratory apparatus, be it remembered, is at certain periods functionally identical with the lungs of air-breathing vertebrates; for the Lepidosiren, after the rains have ceased to flood the river Gambia, finds itself left behind in the mud of the retreating waters; the scorching rays of a tropical sun compel the fish to burrow into the mud, in which it forms a kind of cocoon of hard-baked clay. How is the fish to live in this changed locality? As an inhabitant of the water the respiration was effected by means of its gills alone, as in ordinary fishes; but how is the circulation to be maintained now it is a terrestrial animal? Professor Owen tells us in distinct terms:—"Whatever amount of respiration was requisite to maintain life during the dry months is effected in the pulmonary air-bladders; its short and wide duct or trachea, the œsophageal orifice of which is kept open by a laryngeal cartilage, introduces the air directly into the bladders; the blood transmitted through the branchial arches to the pulmonary arteries is distributed by their ramifications over the cellular surface of the air-bladders, and is returned arterialised by the pulmonary veins. A mixed venous and arterial blood is thence distributed to the system and again to the air-bladders. When the Lepidosiren resumes its true position as a fish, the branchial circulation is vigorously resumed," &c. In the Lepidosiren, then, we have an instance of an animal which is a fish at certain periods of its existence and an amphibian at others; and, as it seems to me, we have in the Lepidosiren a striking illustration of the transition of an organ, originally constructed for one purpose, into one for a wholly different purpose. As Mr. Darwin has said, "All physiologists admit that the swim-bladder is homologous, or ideally similar in position and structure, with the lungs of the higher vertebrate animals;

hence there seems to me to be no great difficulty in believing that natural selection has actually converted a swim-bladder into a lung or organ used exclusively for respiration."* It surely is quite conceivable that under changed conditions, acting for a lengthened period, the Salamandroid Lepidosiren—which some naturalists of note still maintain to be more allied to amphibia than to fish—might gradually convert all its ichthycic characters into amphibian ones, just as I believe it has converted not only the swim-bladder and pneumatic duct into an air-breathing lung, trachea, and glottis, but also two pairs of the gills of the branchial arches into vascular channels, in order that it should be able to maintain a slow circulation, as a terrestrial animal, while encased in its cocoon of mud. I see, moreover, nothing improbable in the supposition that in the Lepidosiren we have a living witness of a fish in a transition stage towards becoming, under favourable conditions, a true amphibian; and I can believe that amphibia are altered forms of fish, to which, in some cases, they bear a considerable resemblance; and I further think it not improbable that one of the steps in the transition—and a most interesting and important step it is—is made by the gradual conversion of the swim-bladder and pneumatic duct into a lung and trachea. Why some fish have a swim-bladder, and others of similar habits have none, can, I believe, be only accounted for by supposing, with Darwin, the absolute independence of new and old structures. So that cases may arise in which a swim-bladder and air-duct may become developed in fishes in which at present they are altogether absent; for Kner has told us that these organs vary considerably even in fishes of the same species, and another naturalist has discovered a rudimentary swim-bladder in some of the Selachiæ. I am not aware that anything is known of the embryology and development of either species of Lepidosiren. A knowledge of the embryology would no doubt throw considerable light on the question of the position of this salamandroid in the animal kingdom; it would show us not only its relation to existing animals, but also its relations to extinct types. Its early embryology would probably reveal to us that at one period of its existence it has no trace of amphibian characters, that the cellular lung and trachea, with the subsequent persistent vascular canals, are not developed in the animal's early stage. Let us hope that some enterprising naturalist will ere long succeed in acquiring a knowledge of the development of the Salamandroid Protopteri.

* "Origin of Species."