

Contributions from the Biological Laboratory of the U. S. Fish Commission,  
Woods Hole, Massachusetts.

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## THE GAS IN THE SWIM-BLADDER OF FISHES.

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The function of the swim-bladder of fishes has attracted the attention of scientists for many centuries. The rôle that this structure plays in the life of the animal has been interpreted in almost as many ways as there have been investigators, and even now there is apparently much doubt as to the true functions of the swim-bladder. Consequently any additional data concerning this organ is of immediate scientific value.

Aristotle, writing about the noises made by fishes, states that "some produce it by rubbing the gill arches \* \* \* ; others by means of the air-bladder. Each of these fishes contains air, by rubbing and moving of which the sound is produced." The bladder was thus considered a sound-producing organ, and it is probable that he arrived at this result by his own investigations.

Borelli\* (1680) attributed to the air-bladder an hydrostatic function which enabled the fish to rise and fall in the water by simply distending or compressing the air-bladder. This hypothesis, which gives to the fish a volitional control over the air-bladder—it being able to compress or distend the bladder at pleasure—has prevailed, to a greater or less degree, from the time of Borelli to the present. To my knowledge, however, there are no investigations which warrant such a theory, while, on the other hand, there are many facts, as shown by Moreau's experiment, which directly contradict this belief. Delaroche† (1807-1809) decidedly opposed the ideas of Borelli, and yet advanced an hypothesis similar to it in many respects. Like Borelli, he said that the fish could compress or dilate the bladder by means of certain muscles, but this was to enable the fish to keep the same specific gravity as the surrounding medium and thus be able to remain at any desired depth (and not to rise and sink). This was also disproved later by Moreau. Delaroche proved that there existed a constant exchange between the air in the air-bladder and the air in the blood, although he did not consider the swim-bladder an organ of respiration.

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\* Borelli, *De Motu Animalium*, 1680. -

† Delaroche, *F., Annales du Mus. d'Hist. Nat.*, tome xiv.

Biot\* (1807), Provençal and Humboldt† (1809), and others made chemical analyses of the gas in the swim-bladder and found 1 to 5 per cent of CO<sub>2</sub>, 1 to 87 per cent of O<sub>2</sub>, and the remainder nitrogen. The most remarkable fact discovered about this mixture was that it frequently consisted almost entirely of oxygen, the per cent of oxygen increasing with the depth of water inhabited by the fish. The reasons for this phenomenon have never been satisfactorily explained.

In 1820 Weber‡ described a series of paired ossicles which he erroneously called stapes, malleus and incus, and which connected the air-bladder in certain fishes with a part of the ear—the atrium sinus imparis. Weber considered the swim-bladder to be an organ by which sounds striking the body from the outside are intensified, and these sounds are then transmitted to the ear by means of the ossicles. The entire apparatus would thus function as an organ of hearing. Weber's views remained practically uncontested for half a century, but recently much has been written both for and against this theory. Whatever the virtues of the case may be, there is certainly an inviting field for further physiological investigations regarding this subject, and more especially on the phenomena of hearing in fishes.

Twenty years later Joh. Müller§ described, in certain Siluroid fishes, a mechanism, the so-called "elastic spring" apparatus, attached to the anterior portion of the air-bladder, which served to aid the fish in rising and sinking in the water according as the muscles of this apparatus were relaxed or contracted to a greater or smaller degree. This interpretation of the function of the "elastic spring" mechanism was shown by Sørensen|| to be untenable. Müller also stated that in some fish, at least, there was an exchange of gas between blood and air-bladder—the latter having a respiratory function—and regarded the gas in the air-bladder as the result of active secretion. In *Malapterurus* he stated that it is a sound-producing organ.

Hasse,¶ in 1873, published the results of his investigations on the function of the ossicles of Weber, stating that their action was that of a manometer, acquainting the animal with the degree of pressure that is exerted by the gases in the air-bladder against its walls. This pressure necessarily varies with the different depths of water which the fish occupies. Hasse did not agree with Weber that the ear is affected by the movements of these ossicles.

One year later Dufossé\*\* described in some fishes an air-bladder provided with extrinsic muscles by whose vibrations sound was produced, the sound being intensified by the air-bladder, which acted as a resonator. He also believed that certain species produced a noise by forcing the gas from the air-bladder through a pneumatic duct.

At about the same time Moreau†† published his classical work on the functions of the air-bladder. He proved by ingenious experiments that many of the prevailing ideas about the action of the air-bladder were erroneous, and that this organ serves to equilibrate the body of the fish with the water at any level. This is not accomplished quickly, but only after sufficient time for the air in the bladder to become

\* Biot, Mémoires de Phys. et de Chimie de la Soc. d'Arcueil, tome I.

† Provençal et Humboldt, Mémoires de Phys. et de Chimie de la Soc. d'Arcueil, tome II.

‡ E. H. Weber, De Aure et Auditû Animalium Aquatiliû.

§ Joh. Müller, Archiv f. Anat. u. Physiologie, 1842, pp. 307 et seq.

|| Wm. Sørensen, Journ. of Anatomy and Physiology, vol. 29, 1894-95.

¶ Discussion of Hasse's theory by Sørensen, op. cit., p. 534.

\*\* Dufossé, Annales d. Sci. Nat., 5<sup>e</sup> sér., tomes 19 and 20, 1874.

†† Moreau, Mémoires de Physiologie, vol. 15, p. 494 et seq.

adjusted to the increase or decrease in external pressure that has taken place. The fish, therefore, makes no use of any muscles in regulating the volume of its air-bladder. The animal can accommodate itself only gradually to considerable changes in depth of water, but can live equally comfortably at varying depths, provided that the change has been gradual enough. Moreau's experiments also convinced him that the gas is actually secreted into the air-bladder, and that there is a constant exchange of gas between it and the blood. In these investigations he has also noticed that section of the sympathetic nerve fibers supplying the walls of the air-bladder hastens the secreting of the gas into the empty bladder. Since then Bohr\* has shown that section of the vagus nerve causes the secretion to cease. Moreau noticed in one fish (*Trigla*) having an air-bladder supplied with muscles that the latter served to make the air-bladder produce sound.

Again, in 1885, the Weberian mechanism was brought to our attention with a new function attributed to it by Sagemehl,† who stated that this mechanism exists not for any auditory purposes nor to tell the animal at what level of the water it is swimming, but to indicate to the fish the variations in the atmospheric pressure. Sørensen tersely contrasts the views of Hasse and Sagemehl by saying that "Hasse considers the air-bladder with the Weberian mechanism as a manometer; Sagemehl regards it as a barometer." The theory of Sagemehl has, naturally enough, met with little favor. Sørensen‡ (1895) held that there is but little evidence for attributing to the air-bladder the function of a lung. It is to be remembered, however, that, according to Sørensen's criterion, no matter what exchange of gases takes place between blood and air-bladder, it can not be considered an organ of respiration "unless its air is renewed by mechanical respiration."

Sørensen also refutes, from anatomical and experimental grounds, the many objections to Weber's theory of the function of the ossicles. He would thus attribute to the air-bladder the function of hearing; indeed, in certain species, the only reason for the survival of the air-bladder is that "the organ is still of acoustic importance; that it acts as a resonator." This idea, Sørensen states, is borne out by the anatomical structure found in *Misgurnus* and *Clarias*, which resembles the celebrated "Colladon resonator." This author attributes to the air-bladder, with its "elastic spring" and various muscular mechanisms, the production of sound as its chief function.

From the foregoing brief historical summary of the function of the swim-bladder it is readily seen that these investigators have not thrown any direct light on the function of the gas itself which is contained in the bladder. It would, indeed, seem strange and contrary to general biological laws for certain gases to exist in the bladder and not be of any use. Why, indeed, should we find a high per cent of oxygen in the bladders of fish taken from 55 to 70 fathoms of water, especially as the gas is actively secreted§ by the fish? Such a specialized expenditure of energy would certainly not be accounted for on the basis of acoustic and phonation functions, as the normal gas composition of the surrounding medium would answer all these requirements. In the voyage of H. M. S. *Challenger*|| it was found that "in the

\* Journal of Physiology, vol. 15, p. 494 et seq.

† Journal of Anat. and Physiology, vol. 29, pp. 544 et seq.: "Theory of Sagemehl," by Sørensen.

‡ Journal of Anat. and Physiology, vol. 29, pp. 109, 205, 390, and 518.

§ J. S. Haldane, Science Progress, vol. 7, 1898.

|| Challenger Reports, vol. 1, pt. 1, p. 226.

deep-sea waters the volumes of oxygen were, in general, less than those calculated from the nitrogen-volumes on the hypothesis of surface absorption of air at the temperature corresponding to the nitrogen found. In waters from great depths the actual volume of oxygen was often very small." "It is worth noting, however, that very small quantities of oxygen present themselves occasionally at moderate depths." Two examples are here given:

Cubic centimeters per liter.		O <sub>2</sub> calculated.	Depth (fathoms).	Per cent of O <sub>2</sub> in dissolved gas.
N <sub>2</sub> .	O <sub>2</sub> .			
15.08	0.6	8.21	2,875	4.33
13.74	1.65	7.15	300	10.72

The *Challenger* expedition did not find any deep-sea waters that were entirely free from absorbed oxygen. In the surface waters the amount of oxygen absorbed from air at a given temperature is the product of its coefficient of absorption into its partial pressure in the undissolved residue. Hence, in surface water, at given temperature and 760 mm. pressure, there would be the following result:

Temperature C.	Dissolved N <sub>2</sub> and O <sub>2</sub> in c. c.		Per cent of O <sub>2</sub> in dissolved gas.
	N <sub>2</sub> .	O <sub>2</sub> .	
0°	15.60	8.18	34.40
35°	8.36	4.17	33.31

In the first table we find the per cent of oxygen in the dissolved gases to be 4.33 per cent and 10.72 per cent respectively, which, compared with the O<sub>2</sub> per cent in surface waters in the second table, shows an enormous deficit. As to the free CO<sub>2</sub> in the sea, I quote again from the *Challenger* report: "From all the evidence afforded by the *Challenger* research we see that free carbonic acid in sea waters is the exception." It would thus seem that there is every condition offered for the elimination of CO<sub>2</sub> from living organism, as by the gills of fishes, and the immediate absorption of this waste product by the surrounding water. It is at least a strange coincidence that with the gradual diminution of oxygen in the water, according to the depth, we find an increase in percentage of oxygen contained in the bladder. Biot cites *Trygla lyra* from 500 fathoms containing 87 per cent oxygen; *Sparus argenteus* from 65 fathoms contained 50 per cent oxygen; *Sparus dentex* from 20 fathoms contained 40 per cent oxygen. My own observations on *Lopholatilus* taken from 55 fathoms showed 66.5 per cent oxygen, and from 70 fathoms showed 69 per cent of oxygen. May not this process be one directly to supply the animal with more oxygen under these conditions, where the oxygen dissolved in the water is so deficient? Such an explanation is tenable, inasmuch as Hüfner, Bohr, Moreau, and Haldane have shown by experiment that the gas is the result of an active secretion in which almost pure oxygen may be given to the bladder.

It occurred to me, if this process existed for the purpose of supplying oxygen to the animal, that changes in the proportion of the constituent gases would be found when the animal was partially or completely asphyxiated, and that these changes

would be fairly constant in all fish subjected to the same conditions. The abundance of squeteague supplied by the Fish Commission Laboratory at Woods Hole furnished the opportunity for a large number of analyses under different conditions. Few analyses had been completed, however, before it was evident that the per cent of oxygen in the air-bladder was no indication of the processes taking place there. In the accompanying table the squeteague numbered 1 to 9 were allowed to become asphyxiated by dying in the open air on the wharf. The animals were very active before they were taken from the live-car. In each case the gas was analyzed at a fixed time after asphyxiation. The bladder was rapidly removed from the dead animal, and a silk ligature was tied a short distance from the small end. The end of the bladder was then amputated, and the 3-way stopper of the Bunte apparatus was inserted into the lumen and fastened by another ligature. The entire Bunte apparatus being filled with water, the first ligature was carefully cut, and the bottom stopper of the apparatus being opened, the gas from the bladder replaced the water in the instrument. The stoppers were now closed and the gas analyzed by the ordinary methods. In No. 4 there was found 17.51 per cent of oxygen, while in No. 6 there was only 6.5 per cent; yet the animals were under practically the same conditions. The amount of  $\text{CO}_2$ , considered independently of the oxygen, also shows no particular characteristic, but when compared with the oxygen it is seen to vary somewhat proportionately with the oxygen; so that, in the two above cases, the quotient of  $\frac{\text{CO}_2}{\text{O}_2}$  became respectively 0.245 and 0.26. It is evident, therefore, that in all nine cases the proportion of  $\text{CO}_2$  to  $\text{O}_2$  is nearly constant, and thus asphyxia has produced a like effect on the gases in the bladder.

This fact naturally suggested analyses of gas taken from normal live animals. The first series were upon animals taken from the live-car and, as far as could be judged, in normal condition. The animals were taken from the water and the gas collected as rapidly as possible. The result of the analyses of this gas is given in the table, Nos. 14 to 20. Here again there is a marked difference in absolute amounts of  $\text{O}_2$  in bladder, and also in absolute quantities of  $\text{CO}_2$ . The extreme differences are shown by comparing Nos. 14 and 20. The  $\frac{\text{CO}_2}{\text{O}_2}$  coefficient, however, shows a close agreement throughout the seven specimens subjected to the same conditions. Even in these experiments the chances for partial asphyxiation were not entirely eliminated, for this would begin during the time that the gas was being collected. Another set of experiments was made on squeteague in which the gas was collected while the gills of the animals were irrigated with salt water, thus giving no possible chance for asphyxiation; the results are given in Nos. 21 to 23 of the table. In this experiment, as in the two previous ones, there are differences in absolute amounts of  $\text{O}_2$  and  $\text{CO}_2$  in the different specimens, but the  $\frac{\text{CO}_2}{\text{O}_2}$  quotients are very nearly the same.

Another series of experiments is recorded in Nos. 10 to 13. These squeteague represented different stages of asphyxiation. None were dead, but none were very active. The result of the analysis showed a  $\frac{\text{CO}_2}{\text{O}_2}$  quotient, which is especially interesting, for it varied with the condition of the animal. In No. 10 the  $\frac{\text{CO}_2}{\text{O}_2}$  quotient

was 0.122, which corresponds with the series beginning with No. 14, and this animal was the most active. In No. 12 the  $\frac{\text{CO}_2}{\text{O}_2}$  quotient was 0.191, which corresponds to the first series, and of the three this animal was the nearest dead.

The table records the result of the various analyses as they were made in 1900. In the summer of 1901, at my request, both Mr. E. H. Green and Mr. A. K. Krause, independently of each other, made analyses of the gas taken from animals subjected to the same conditions as described above. In both cases the  $\frac{\text{CO}_2}{\text{O}_2}$  quotients fell in their respective places in the series.

If we now compare the  $\frac{\text{CO}_2}{\text{O}_2}$  quotients in Nos. 1 to 9 as representing asphyxiated animals, and the quotient in Nos. 21 to 23 as representing animals in their normal condition, it will be seen that there is a great difference between them. These results indicate that there is an active respiratory process taking place in the bladder during asphyxiation.

No.	Per cent O <sub>2</sub> .	Per cent CO <sub>2</sub> .	$\frac{\text{CO}_2}{\text{O}_2}$ .	Remarks.	No.	Per cent O <sub>2</sub> .	Per cent CO <sub>2</sub> .	$\frac{\text{CO}_2}{\text{O}_2}$ .	Remarks.
1	14.45	3.99	0.275	Gas taken after the animals had been asphyxiated by dying on the wharf.	14	19.00	2.30	0.121	Gas removed while animals were alive, immediately after being taken from car.
2	15.85	4.47	.282		15	13.30	1.28	.096	
3	15.80	4.70	.297		16	10.08	1.26	.125	
4	17.51	4.30	.245		17	8.34	.93	.115	
5	15.91	4.20	.264		18	10	.82	.082	
6	6.50	1.60	.261		19	8.60	.62	.072	
7	15.64	4.54	.290		20	5.55	.70	.126	
8	12.20	3	.247						
9	9.70	2.90	.298		21	11.86	.75	.063	
10	18.80	2.30	.122	22	12.12	.75	.061		
11	16.90	2.50	.147	23	8.77	.92	.104		
12	12.00	2.30	.191	Gas removed when animals were almost dead in a crowded car.					Spinal cord cut and gas removed.
13	17.80	2.80	.157		24	11.40	1	.087	

## SUMMARY.

1. The evidence for exchange of gases between blood and air-bladder must be sought not in the absolute amount of O<sub>2</sub> or CO<sub>2</sub> in the bladder, but in the proportion of these two gases.

2. The  $\frac{\text{CO}_2}{\text{O}_2}$  quotient of the gas in the swim-bladder of normal animals is small, ranging from 0.06 to 0.10.

3. The  $\frac{\text{CO}_2}{\text{O}_2}$  quotient increases as the animal is asphyxiated, and reaches 0.24 to 0.29 when killed by this means.

4. The fact that different per cents of O<sub>2</sub> are found in different squeteague under the same conditions strengthens the view that the gas is a secretion; for how could we have 19 per cent in No. 14 and 5.55 per cent in No. 20 under a process of diffusion?

5. Fish (*Lopholatilus chamaeleonticeps*) from 55 fathoms of water have 66.5 per cent of O<sub>2</sub> and only a trace of CO<sub>2</sub>, and from 70 fathoms of water have 69 per cent of O<sub>2</sub> and a trace of CO<sub>2</sub>. The deeper the water the smaller the  $\frac{\text{CO}_2}{\text{O}_2}$  quotient. This goes on until pure oxygen alone is present in the air-bladder.