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Notes on the Structure and Mode of Action of the "Oval" in the Pollack (Gadus pollachius) and Mullet (Mugil chelo).

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With Seven Figures in the Text.

DURING the summer of 1911 I conducted at the Plymouth Biological Station a series of experiments on the living active gas-gland associated with the bladder of certain marine fish, the results of which are recorded in a paper published in the Anatomischer Anzeiger for 1911 (Bd. XL, p. 225). Whilst so employed I incidentally made some observations on the structure and mode of action of the "oval" in fishes, and since my conclusions differ in several particulars from those of Nusbaum and Reis (Bull. Acad. d. Sciences Cracovie, 1905, p. 778; Anatomischer Anzeiger, Bd. XXXI, 1907, p. 169), I think it as well to put them on record. Most of my observations were made on the Pollack. If a weight be attached to this fish so as to cause the gas-gland (oxygen gland) to become active and to pump oxygen into the bladder, it will be found that the oval strongly contracts, so as to prevent the additional gas forced into the bladder from escaping into the blood. The oval, it may be mentioned, is a large oval area usually situated in the dorsal posterior wall of the bladder. It differs from the rest of the bladder wall in that it alone is permeable to the contained gases, and, like the ductus pneumaticus in Physostomi, permits their escape when the conditions require it. In the Pollack the oval is normally widely open and is invisible to the naked eye, but on the gas-gland being caused to become active in an unusual degree, the oval becomes strongly contracted and is then a very conspicuous structure inside the bladder. This contraction of the oval is of course effected by muscles, and the result of it is to cause the thin-walled permeable area to become more or less completely shut off from the general bladder cavity, the walls of which, as just mentioned, are impermeable.

According to the observations of Nusbaum and Reis on the ovals of Perca, Lucioperca, and Ophidium, the oval has the following structure:—The ordinary wall of the bladder is composed of three

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layers : an inner elastic and muscular layer covered internally by the squamous epithelium lining the bladder cavity, a middle conjunctive and vascular layer, and an outer fibrous layer. At the periphery or edge of the oval there is developed a special band of circular smooth muscle fibres, which by contraction can lessen and obliterate altogether the area of the oval exposed to the gases in the general bladder cavity. Over this area, limited externally by the circular band just mentioned, the inner layer is quite absent, only the squamous epithelium being present, and this latter in consequence abuts directly on the middle layer, in which, in the oval area, the capillary system is much developed.* In the region of the oval, therefore, the gases contained in the bladder can come into very close contact (only separated by the squamous epithelium) with the numerous capillaries of the oval contained in the middle layer. Attached to the edge of the oval, immediately external to the circular muscle band, are numerous radial muscle fibres (belonging to the inner layer surrounding the oval), the function of which is to act in opposition to the circular band and enlarge the oval area. The foregoing statements and the mode of action of the oval, according to Reis and Nusbaum, are illustrated by Figures 1-4 (devised from the statements and diagrams of these authors). It will be seen that, according to these authors, the closure of the oval, in the fishes studied by them, is effected by the simple contraction of the circular muscle band (the radial muscles slackening), the squamous epithelium being thereby raised from contact with the blood-vessels and separated from them by the muscles. I presume that these statements of Nusbaum and Reis are based upon the study of actual sections of closed and open ovals; otherwise I should doubt their accuracy, because this mode of action of the oval is quite unlike that of the oval in the Pollack and the Mullet, because I find it difficult to believe that the squamous epithelium ever becomes separated from the capillary plexus in the manner asserted, and finally because, if Tracy (Anat. Anzeiger, 1911) is correct in his interesting view that the oval is homologous with the posterior chamber of the Carp bladder and the distal part of the ductus pneumaticus of Physostomi (Fig. 7), these statements are improbable a priori. It is evident that if the edge of the oval is homologous with the circular edge of the septum separating the anterior and posterior chambers of the Carp or Siphonostoma bladder, then it might naturally be anticipated that the

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^{*} The so-called "wundernetz"—a bad term, since this special capillary development has nothing to do with the rete mirabile duplex situated on the artery and vein supplying the gas-gland (vide my Anat. Anzeiger paper already mentioned and Proc. Zool. Soc., Lond., 1911, p. 183).

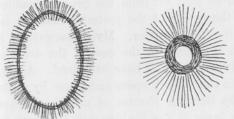


Fig. 1 Open Oval (Surface View). Fig. 2. Semi-closed Oval. Radial Muscle Sq. epithel. Circ.Muscle Inner Layer 00000000000 Middle Layer FOuter Layer Fig. 3. Open Oval (in section). Capillary plexus 2 Sq. epithel. 1082B (1920) -Rad. Muscle Capillary plexus Fig. 4. Closed Oval (in section). The squamous epithelium is separated from the capillaries. Diagrams adapted from the description & diagrams of Nusbaum & Reis. Carp, &c. Posterior Chamber represents dilated distal end of ductus prieumaticus with posterior opening. Posterior Chamber Gurmard, Toad-fish, Siphonostoma, &c. Proximal portion of ductus disappeared Cavity of Oval (homologous with posterior chamber of bladders of other fish) All tish with ovals.

Fig. 5. Derivation of Oval, according to Tracy.

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oval area would be shut off from the general bladder cavity in the same way that the cavity of the posterior chamber is shut off from the anterior in the Carp bladder. My investigations prove that this last anticipation is correct in the case of the ovals of the two fish (Pollack and Mullet) which I have examined. As shown by Figs. 5 and 6, the oval in the Pollack opens and closes by means of a circular fold which works like the shutter of an iris diaphragm. The impermeable inner layer of the bladder wall is shown by a thick line, and, as the figures indicate, this ceases at the edge of the open oval, the oval area merely being covered by the thin layer of squamous epithelium. As the figures also indicate, the circular fold is formed by the actual rotation of the tissue round the edge, hence the more closely shut the oval the deeper is its cavity. This deep cavity of the closed or nearly closed oval is very obvious in the actual bladders of the Pollack, Mullet, and other fish, but, according to the statements of Nusbaum and Reis, it does not exist in the species they examined. I am, of course, quite ready to admit that all ovals may not work on the same principle-in Dactylopterus volitans, e.g., I find that the oval-like structure has in section an appearance different in several particulars from that of the normal oval; at the same time. I shall feel more satisfied that the mode of action of the oval in Perca, Lucioperca, and Ophidium is different from that of the oval of Gadus, Mugil, and other fish, if Nusbaum and Reis would supply us with figures constructed from observations of actual sections of the open and closed oval instead of mere diagrams which, to say the least, look very hypothetical. The figure of the open oval of Lucioperca published by Reis (Kraków, Rozpr. Akad., 1906, pp. 639-670) is of little use as evidence in the present connection.

I must point out, in conclusion, that, literature being not easily accessible in the centre of India, papers bearing upon the above subject may have been published without my knowledge since I left University College, London. I must also confess that I am unacquainted with the exact nature of the controversy concerning the oval between Nusbaum and Jaeger. Possibly Jaeger has already stated the objections I have urged above. If so, he has not confirmed them with figures. Finally, I may mention that I have exhibited my own sections of the open and closed oval at the Royal Institution of London, where they were examined by several zoologists of repute.

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