The Structure and Function of the Gas Bladder in 
Argentina silus 
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With one plate (fig. 1)

SUMMARY

Anatomical and histological observations were made on the gas bladder of the soft-
rayed marine salmonoid fish Argentina silus, which usually lives at depths of about 200 
m. The gas bladder is completely closed but rather unlike other known types of closed 
gas bladders. It is composed of three tissue layers, which may conveniently be called 
mucosa, submucosa, and tunica externa. The latter contains a large amount of guanine. 
The tunica externa is penetrated by numerous blood-vessels, which form a widely 
distributed rete mirabile of a peculiar 'bi-dimensional' type in the submucosa. All 
vessels reaching the mucosa seem to come from this rete system, and no special 
'resorbent mucosa' such as occurs in euphysoclistae could be identified. The mucosa 
is folded, forming an alveolar-like structure of unknown function. The gas gland layer 
is separated from the lumen of the bladder by smooth muscles and an inner epithelium. 
The close anatomical association of the gas gland tissue with smooth muscles probably 
is of importance for gas secretion. Analyses of gases from specimens taken from a 
depth of about 80 m showed a mean oxygen value of almost 80%, which indicates 
a similar gas secretory mechanism to that in euphysoclistae. Certain aspects of the 
physiology of the gas bladder in relation to life in deep water are shortly discussed, and 
the need for a thorough histological examination of the gas bladder in deep-water 
salmonids is emphasized.

INTRODUCTION

FISHES living below depths of 500 to 1,000 m usually have no gas 
bladder or have this converted into a fat storage organ (Marshall, 1954). 
Obviously below a certain depth inflation of a gas bladder is physiologically 
impossible owing to the water pressure. So far as deep-sea fishes have a func-
tioning gas bladder, this is of the closed type. Even among the predominantly 
physostomatous order Isospondyli the deep-living forms have no pneumatic 
duct (Jones and Marshall, 1953). An exception are the deep-living fresh-water 
salmonids which have a pneumatic duct. As may be expected, the gas bladders 
in deep-sea fishes show certain anatomical features which might be considered 
as adaptations to their environment. Thus in Gonostomatidae, Sternopyty-
chidae, and Myctophidae the gas gland and the rete mirabile are larger than 

The present investigation has been devoted to the gas bladder of Argentina 
silus (suborder Salmonoidea of the Isospondyli). This fish lives at depths 
between 200 and 550 m 'along the edge of the continental platform' (Murray 
and Hjort, 1912). It is known to have a closed gas bladder (de Beaufort, 1909; 
Fänge—Gas Bladder in Argentina silus

Jones and Marshall, 1953), but the more detailed anatomy of this organ does not seem to have been studied before.

**Material and Methods**

The material consisted of five small specimens (body length 28–30 cm) taken by trawling from a depth of about 80 m, which is unusually shallow for the species. At the time of capture the gas bladder had exploded in two specimens but was apparently undamaged in the other three. The fishes were all dead or moribund. Samples of gases were taken immediately after the fishes were caught and were analysed on board the investigation ship. For the analyses the Krogh micro gas analysing apparatus was used (Fänge, 1953). Dissections were made on fresh, unfixed specimens. For histological examination the gas bladders or parts of them were fixed in Bouin's fluid. Paraffin sections were stained with Azan or with haematoxylin and eosin.

**Results**

**Gross Anatomy**

The gas bladder is slender and spindle-shaped (fig. 1, A). In the specimens investigated (not fully grown) the length of the bladder was 10–14 cm. Beneath the peritoneal cover the bladder has a silvery, shining appearance. The organ is almost perfectly circular in transverse section.

Many blood-vessels pass to the gas bladder from the region of the large dorsal vessels (fig. 2, B). Six to ten large vessels were seen on each side. It was not possible to determine which of these vessels were arteries and which were veins, because the soft, oily consistency of the body-tissues made macroscopic studies difficult. No connexion could be observed between the gas bladder vessels and the hepatic portal system. The blood-vessels reaching the bladder branched over its surface (fig. 2, B), and the branches passed into the interior of the bladder-wall through numerous small transverse 'clefts'. The internal surface of the bladder was folded in a characteristic manner, forming alveolar-like structures somewhat reminiscent of a honeycomb (fig. 2, A). The folds were restricted to the mucosa and did not involve the external parts of the bladder-wall.

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**Fig. 1 (plate).**

A, the isolated gas bladder. Note the absence of pneumatic duct and the metallic appearance due to guanine. The numerous small 'clefts' are entrance places for blood-vessels.

B, transverse section through the bladder-wall. In the submucosa numerous rete mirabile bundles are seen. The tunicia externa has a striated appearance. (Haematoxylin-eosin.)

C, surface preparation of the unstained mucosa. Winding capillary loops are seen. A few rete mirabile bundles are indistinctly visible (upper left).

D, longitudinal section showing a mucosal fold belonging to the alveolar-like structure of the mucosa. The muscularis mucosae at this place consists mainly of circularly arranged fibres. (Azan.)

E, transverse section. In the lower part of the figure submucosa is seen, with several rete mirabile bundles. (Azan.)

F, transverse section. At this place the muscularis mucosae contains both circularly and longitudinally arranged smooth muscle-fibres. The glandular layer is poorly developed and indistinctly seen. (Azan.)
Microscopic anatomy

It is often possible to distinguish three layers in the wall of the gas bladder: tunica externa, submucosa, and mucosa (Fänge, 1953; O’Connel, 1955). In Argentina these layers stand out very clearly. Outside the tunica externa there is a ventral peritoneal cover; thus the gas bladder is situated retroperitoneally.

The tunica externa. The external two-thirds of the bladder-wall consist of a dense connective tissue layer probably corresponding to the tunica externa of other species. Immediately below the peritoneum the tunica externa has a loose fibrous texture and contains large blood-vessels mainly longitudinally arranged. The major part of the tunica externa consists of a dense lamellar connective tissue loaded with guanine. The guanine lamellae run circularly more or less like barrel-hoops in the bladder-wall. At rather regular intervals (30–100 μ apart from each other) blood-vessels pass through the tunica externa perpendicularly to the connective tissue lamellae. The penetrating blood-vessels are surrounded by their own connective tissue sheaths consisting of collagenic membranes. The heavy deposit of guanine in the gas bladder of Argentina has previously been mentioned by Voit (1865), according to whom guanine crystals from the gas bladder of A. sphyraena have been used to manufacture pearl essence for making artificial pearls. Probably owing to an abundance of guanine lamellae the tunica externa in histological sections has a characteristic striated appearance (fig. 1, B). The occurrence of guanine in the wall of the gas bladder is also known from other fishes, for instance clupeids (Maier and Scheuring, 1923).
The submucosa. This is a layer of very loose connective tissue situated between the tunica externa and the mucosa. In this layer there occur numerous ribbon-like bundles of small blood-vessels (fig. 1, B, E, F). They are oriented mainly in a longitudinal direction. Each bundle consists of a single row of alternating arterioles and venules. The bundles constitute a sort of rete mirabile which is described further on in the text.

The mucosa. The mucosa consists of a very thin inner epithelium, a smooth muscle-layer ("muscularis mucosae"), and a glandular layer. The muscularis mucosae is composed of bundles of smooth muscles arranged both circularly and longitudinally. At certain places the smooth muscle-layer is thickened, forming the alveolar structures mentioned above (fig. 2, A). The glandular layer is richly vascularized by winding capillary loops coming from the rete mirabile bundles (figs. 1, C; 4). The glandular cells are irregularly shaped and often look more like modified connective tissue cells than epithelial cells. They are often binucleate, and some of the cells are very large and contain deformed or fragmented nuclei. Their cytoplasm is finely granulated and stained reddish by Azan. Often the cytoplasm is highly vacuolated (fig. 4). In its general appearance the glandular layer resembles to a considerable extent the glandular layer of the gas bladder in cyprinids (Fänge and Mattisson, 1956). Like this it is separated from the lumen of the gas bladder by a smooth muscle-layer and the inner epithelium.

The rete mirabile. The bi-dimensional arrangement of the vessels composing the rete mirabile is typical of Argentina and has hitherto not been observed in any other fish, although the caudal part of the rete mirabile in the cyprinid
gas bladder has a somewhat similar structure. Alternating arterioles and venules are situated close together in single rows. Such flat bundles usually consist of 6 to 10 vessels but as many as 16 to 18 may be counted, while the smaller bundles are composed by only two vessels—a small artery and its accompanying vein. The two-vessel bundles are formed by successive dichotomous division of larger bundles. At their distal ends the two-vessel bundles continue as capillary loops winding in the glandular layer (figs. 1, c; 5).

The arterioles of the rete mirabile have a varying appearance. In some bundles they have thin walls and are almost indistinguishable from the adjacent venules (fig. 3, A). In other bundles the arterioles have thick walls (fig. 3, B), and often their endothelium is folded with nuclei protruding into the arterial lumen (fig. 3, C). The latter structure might indicate that the arterioles are able to contract and shut off the rete circulation by action of their smooth muscles. The rete mirabile bundles containing thick-walled arterioles are for the most part situated near the tunica externa and the bundles containing thin-walled arterioles near the mucosa. It may be recalled that supposedly contractile arterioles are found in the proximal part of the rete mirabile of euphysoclistae (Fänge, 1953, p. 30). Those parts of the rete mirabile where the arterioles have thin walls are certainly better suited for diffusion processes than those containing thick-walled arterioles.

In a transverse section 8 μ thick through the anterior part of the gas bladder, which is 5 mm thick at this point, 144 bundles were counted and in another...
similar section 122 bundles. If we assume a mean of 10 blood-vessels in each bundle, there are thus more than 1,000 individual vessels cut in a single histological section. Now blood-vessels penetrate the tunica externa along the whole length of the bladder, giving rise to rete mirabile bundles in the underlying submucosa. Thus the number of over 1,000 has to be multiplied by a factor of perhaps about 50 (the exact number can only be found by reconstruction studies) in order to give the absolute amount of individual blood-vessels participating in the rete mirabile. The value 50,000 arrived at by this rough calculation is of course very uncertain, but it is interesting that it is similar to that calculated by Krogh (1936) for the well-developed rete mirabile of the eel (196,000 individual blood-vessels).

The composition of the gases contained in the bladder

As a rule the gas bladder of fishes living in deep water contain a high percentage of oxygen. That this is also true for *Argentina* is shown by the values from three specimens given below:

<table>
<thead>
<tr>
<th>No.</th>
<th>Carbon dioxide, %</th>
<th>Oxygen, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0·8</td>
<td>74·7</td>
</tr>
<tr>
<td>2</td>
<td>0·8</td>
<td>77·7</td>
</tr>
<tr>
<td>3</td>
<td>0·8</td>
<td>79·8</td>
</tr>
<tr>
<td>Mean values</td>
<td>0·5</td>
<td>77·4</td>
</tr>
</tbody>
</table>

**DISCUSSION**

The results from the gas analyses show that in the closed gas bladder of *Argentina* there occurs a gas secretion similar to that in euphysochloristae,
producing a gas mixture rich in oxygen. In all fishes which are able to inflate their bladders by so-called gas secretion, there are vascular specializations of rete mirabile type. Even in cyprinids, where gas secretion is a very slow process, there are rete mirabile formations (Fänge and Mattisson, 1956), although composed of few vessels. In Argentina the rete mirabile is of an uncommon type, but it consists of many thousands of vessels and obviously has a large functional capacity. Most probably a rete mirabile is a necessary equipment for the process of gas secretion. (For a discussion of its role see, for instance, Maetz, 1956.) Scholander (1954) showed that the rete mirabile provides a counter-current diffusion barrier against oxygen loss through the blood leaving the bladder.

In euphysoclistae there can be distinguished two parts of the mucosa, a secretory part and a resorbent part, each with its own type of circulation. The secretory mucosa is furnished with blood from the rete mirabile while the resorbent mucosa is vascularized by a non-rete system. In Argentina all the blood supply to the mucosa probably comes from the rete mirabile bundles. This must provide a good protection against losses of oxygen from the bladder. Certainly the wide distribution of rete mirabile bundles in the submucosa of the Argentina gas bladder is a special adaptation to deep-sea life. The function of the alveolar-like structure of the mucosa is enigmatic. It may be mentioned in this connexion that similar alveolar-like mucosal structures have been observed in certain other fishes belonging to the order Isospondylia (Megalops, Engraulis, &c.) (de Beaufort, 1909). The abundant guanine lamellae in the tunica externa perhaps gives protection against the disappearance of gases from the bladder.

Whereas Argentina, like other deep-water marine fishes, has a closed gas bladder, the coregonids that inhabit fresh water are physostomatous. The deep-water coregonids are peculiar in that they have a very low oxygen content in their gas bladder (Hüfner, 1892; Scholander, 1956).

No gas gland or rete mirabile has been observed in Coregonus and other salmonids, but Corning (1888) observed that the anterior part of the gas bladder in Salmo is richly vascularized near the entrance of the pneumatic duct. Perhaps a thorough histological examination of the gas bladder in salmonids would reveal at least in certain species the existence of rete mirabile bundles reminiscent of those in Argentina, although less numerous. The observation by Saunders (1953) that in Coregonus clupeaformis taken from shallow water the gas bladder occasionally contains as much as 42.3% of oxygen strongly suggests that there exists in salmonids a gas secretory mechanism not greatly unlike that of other fishes. But how can the high nitrogen percentage and the low oxygen percentage in the gas bladder of coregonids taken from deep water be explained? Powers (1932) has proposed a theory according to which gases are added in small quantities to the bladder by means of bubbles, independently of the partial pressure in the gas bladder. Owing to their greater diffusibility through living membranes, carbon dioxide and oxygen are more easily reabsorbed by the blood than the inert gases.
According to the author's observations bubbles are formed in clefts and ducts of the gas gland in Ctenolabrus, Spinachia, and other euphasoclistae during gas secretion (Fänge, 1953). However, no clefts or ducts are known from the gas bladder mucosa of such fishes as salmonids, cyprinids, and Argentina.

In Argentina there is an intimate association between the gas gland tissue and the smooth muscle-layer (muscularis mucosae). Such a close association of gas gland tissue with smooth muscles is of general occurrence and has been found in many different fishes (Fänge and Mattisson, 1956). Probably it is of importance for gas secretion, because this seems always to be correlated with relaxation of the smooth muscles. One possibility is that the movements of the muscularis mucosae could have a mechanical effect upon the release of newly formed gas bubbles into the bladder. Hagman (1952, personal communication) has used hot mercuric chloride fixative for the demonstration of gas bubbles in active gas glands. Unfortunately he died without publishing his results. Certainly his technique would be of value for further studies of the process of gas secretion.

REFERENCES

Hagman, N., 1952. Personal communication.