A CINERADIOGRAPHIC STUDY OF THE CENTRAL CIRCULATION IN THE HAGFISH, *MYXINE GLUTINOSA* L.

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(With Plate 10)

Since Müller (1835) published his pioneer monograph on the morphology of myxinoids, scientists have shown great interest in these phylogenetically important forms. Although works have been presented unabated since then, very few deal with the physiology of these species and almost nothing is known regarding the functioning of their circulatory system.

Retzius (1890) demonstrated the existence of an accessory heart shunted into the venous hepatic circulation and named it the portal heart. He also described and demonstrated the caudal hearts on the venous side in the tail region of *Myxine*. In 1926 Cole demonstrated a similar structure on the deep anterior cardinal vein and termed it the cardinal heart. Recently Johansen (1960), by means of pressure recordings in the vascular system of *Myxine*, presented results that demonstrated an active role of the gills in the propulsion of arterialized blood. Cole (1907) and Hofbauer (1937), among others, have demonstrated histologically the existence of large striated muscle fibres in the gill sacs of this species. Further, the heart of myxinoids is unique among all vertebrate hearts in having no cardioregulatory nerves (Fänge & Østlund, 1954; Greene, 1902; Carlson, 1904; Jensen, 1958). The present study introduces modern radiological methods for the study of the central circulation in *M. glutinosa*.

MATERIAL AND METHODS

The specimens of *M. glutinosa* used for this study were trapped near the Dröbak Biological Station in the Oslofjord in Norway. Only large, adult specimens were used, and they were kept in aquaria with running sea water of 4–7° C. During the experiments the animals were immobilized on a sheet of rubber and immersed in a lucite box filled with cold sea water. The lucite box was easily penetrated by the radiation necessary for the examination. The roentgen equipment consisted of an under-couch tube and a Phillips image-intensifier connected with an Arriflex camera which was operated at a speed of 26 frames per sec. (Johansen & Hol, 1960).

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An incision was made on the ventral side in the posterior part of the animal and the post-cardinal vein was exposed. A polyethylene catheter (P.E. 10) was inserted into the vessel in cephalad direction. Through this catheter the contrast medium was injected under fluoroscopic control. The contrast medium used was 45% Hypaque in doses of around 0·5 c.c. As the animals were surrounded by water their contours were not visible on the films.

<div align="center">OBSERVATIONS</div>

Following a contrast injection, the sinus venosus and atrium became discernible (Pl. 10, fig. 1 A). These heart chambers are comparatively large and situated well to the left with the atrium entirely dorsal to the sinus venosus. Thus the pictures of these chambers will overlap each other (Fig. 1 A, B) but during contraction of the atrium the sinus venosus is better visualized (Fig. 1 B, C). The sinus venosus seemingly consists of two compartments, one anterior and one posterior, both somewhat rounded and separated by a small indentation on the left lateral contour (Fig. 1 B). By the force of the contrast injection, and probably also from the contraction of the sinus venosus and atrium, there occurred some filling of the hepatic veins and the jugular or left anterior cardinal veins (Fig. 1 A–C). The ventricle is median and slightly to the right and was filled during the contraction of the atrium and sinus venosus (Fig. 1 B, C). Neither the sinus venosus nor the atrium showed complete emptying but the residual volumes can be calculated to be less than half of the diastolic contents. The contraction of the ventricle (Fig. 1 D) resulted in a considerable but not complete emptying. Following ventricular contraction, the ventral aorta and afferent branchial arteries were filled. The latter may be seen to end at the posterior lateral aspect of the gill bodies (Fig. 1 D, E). Heart frequencies varied widely from specimen to specimen with average rate of around 30 beats/min.

    This study was primarily initiated because of the evidence from earlier work (Johansen, 1960) that the gills and the muscles in the branchial region take active part in the blood circulation. Outer examination as well as fluoroscopic inspection of the branchial region in *Myxine* revealed that the striated musculature in this region showed repeated contractions. Followed by the high-speed cineradiography, these movements could be resolved and analysed. Fig. 1 A, B, shows faintly the gill bodies and the dorsal aorta outlined by contrast from an earlier test injection. The gills are seen oblique and somewhat flattened, corresponding with a contraction of the gill bodies. This position may also be seen directly upon opening of the branchial region. In Fig. 1 C, the gills are seen in their early resting phase and the contrast in the dorsal aorta has disappeared. Fig. 2 A–D shows the sequence of events during contraction of the gill bodies. In Fig. 2 A the gill bodies are relaxed and the contrast uniformly distributed. The dorsal aorta is well defined to the left in the picture. Fig. 2 B–D shows progressively the different phases of a contraction. The gill bodies are reduced in size and the contrast in the efferent branchial arteries and the dorsal aorta is squeezed in peripheral direction. Fig. 2 E shows the gills relaxed and the dorsal aorta refilled.

    Some elucidation of the intricate problem of the existence of extravasation in

vertebrates is provided by this study. It seems to be generally accepted that the circulatory system in myxinoids must be considered a semi-closed system, where lacunar spaces (blood sinuses) at some particular sites constitute the means of communication between arteries and veins (Cole, 1926; Marinelli, 1956). Thus the gills in *Myxine* are surrounded by such blood sinuses, the peribranchial sinuses (Cole, 1926). On one occasion we had the opportunity to see the peribranchial sinuses filled with contrast. The afferent path of the contrast medium, injected as usual through the post-cardinal vein, is very difficult to ascertain, but it showed up as a result of overloading the central vessels with contrast. In Fig. 3 the peri-branchial sinuses are visible as a number of crescents bordering the gill bodies laterally. Fig. 3 demonstrates the events during contraction of the body-wall muscles in the branchial region. The contraction is followed by a discernible reduction in the amount of contrast in the sinuses. The figure also demonstrates some phases in the muscle contraction. In Fig. 3 A, B the contraction starts with a twisting and slight reduction of the diameter. Then follows a shortening and broadening, especially of the distal part (Fig. 3 C). The movements end in the resting phase with a stretching and narrowing of the region (Fig. 3 D, E).

DISCUSSION

The data presented in this study give evidence to support the hypothesis that the circulatory system in *Myxine* is first of all characterized by a decentralization of the blood-moving power from the heart to the gills and branchial muscles and the earlier-found auxiliary hearts on the venous side of the circulation (Johansen, 1960). Following each gill contraction, blood inside the gill bodies as well as blood in the efferent arteries is expelled peripherally into the dorsal aorta. Further, our results confirm the existence of a direct communication between the vascular vessels and the lacunar spaces in *Myxine* and support our assumption that contraction of the body-wall muscles in the branchial region has an emptying effect on the peri-branchial sinuses. Additional information is gained from this study regarding the functioning of the branchial heart *in situ*. It may be emphasized that the heart in *Myxine* possesses a rather high emptying power for all the chambers.

A study using radiological methods was presented by Mott (1950) studying the circulation in the common eel, *Anguilla anguilla*. Contrary to the finding of Mott for *Anguilla*, our study revealed no pulsations in the bulbous aorta of *Myxine*.

SUMMARY

1. An angiocardiographic study has been made of *Myxine glutinosa*, using modern cineradiographic instrumentation. In addition to the heart, vessels in the branchial region have been studied.

2. The topography of the heart chambers and their filling and emptying have been described. The frequency of the heart at body temperature, 8–10° C., was found to be about 30 beats per minute.

3. Results are presented that support the assumption that the gill sacs and their

ducts, as well as striated muscles in the branchial region, take an active part in the propulsion of blood.

4. The phenomenon of extravasation or circulation in lacunar spaces (blood sinuses in direct communication with the true blood-vessels) has been demonstrated. The described muscular activity in the branchial region seems to promote the return of blood from these sinuses to the heart.

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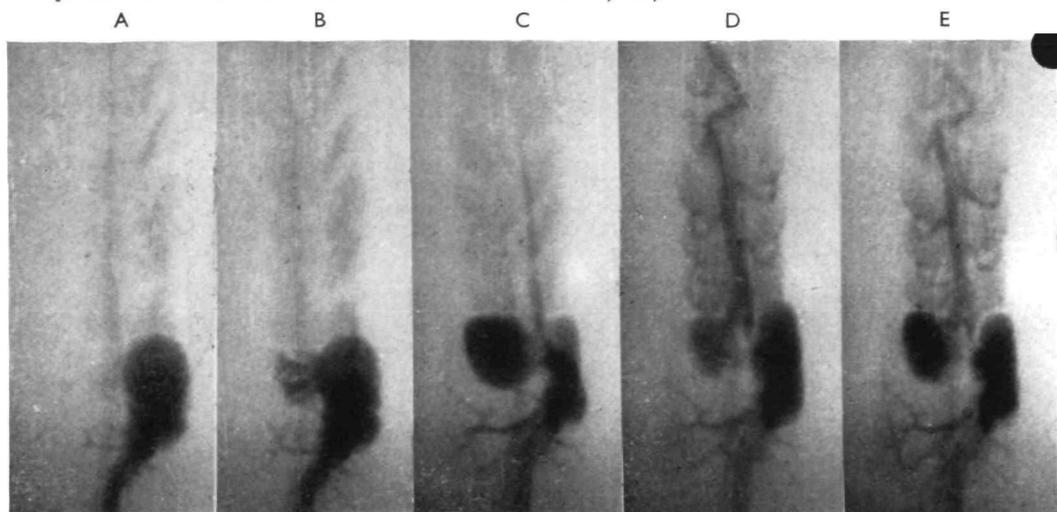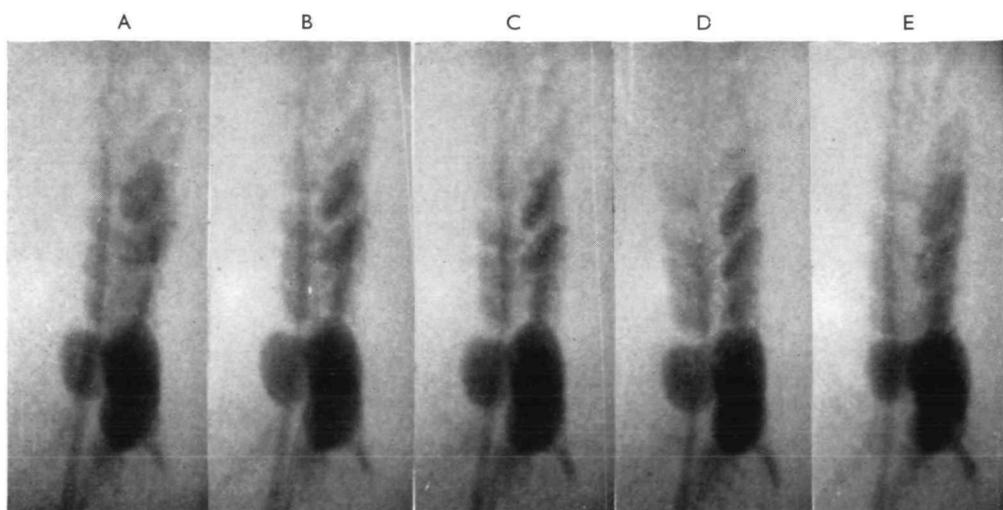RETZIUS, G. (1890). Ein sogenanntes Caudalherz bei *Myxine glutinosa*. *Biol. Untersuch.* **1**, 94.
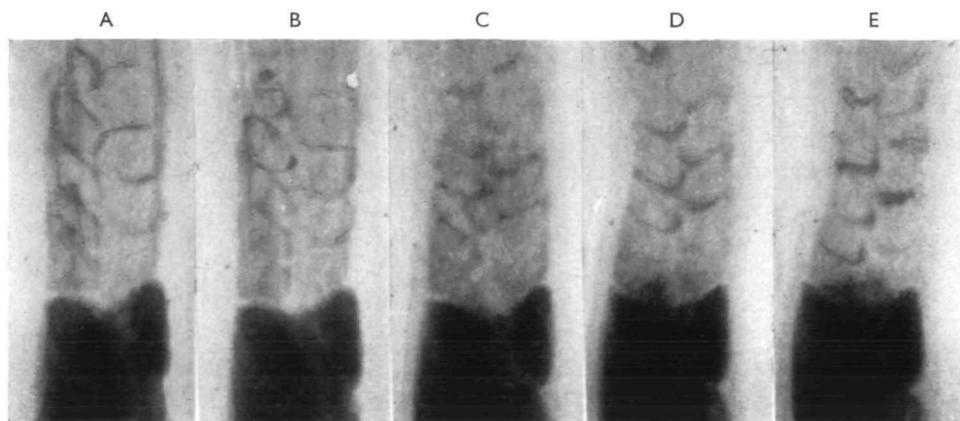
Fig. 1

Fig. 2

Fig. 3

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EXPLANATION OF PLATE

Fig. 1. Angiocardiography of *Myxine glutinosa* (ventral aspect). A. Filling of the sinus venosus and atrium. A few liver branches are seen filled retrogradely. Contrast medium from a test injection faintly outlines the gill bodies and the dorsal aorta running to the right of the atrium. B. Early filling of the ventricle and slight inflow to left jugular and liver veins. Note the left lateral indentation on the sinus venosus. C. The atrium is seen contracted and the ventricle filled; the sinus venosus is also contracted and well outlined. D. Contraction of the ventricle resulting in filling of the ventral aorta and the afferent gill arteries. E. A new atrial contraction fills the ventricle with contrast medium. F. Schematic drawing of the heart and vessels in the branchial region.
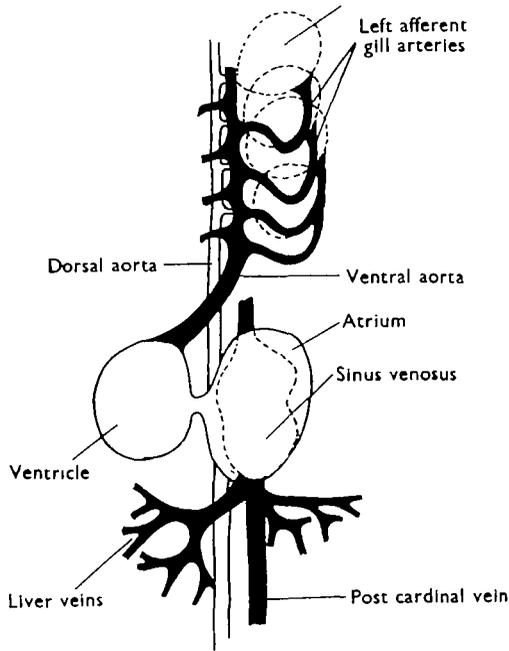

Fig. 1 F

Fig. 2. Gill contraction. A and E. Relaxed gills. B–D. Show progressively different phases of a gill contraction resulting in an emptying of the efferent gill vessels and the dorsal aorta. The amount of contrast medium in the gill bodies is considerably reduced.

Fig. 3. Overloading of the central veins resulting in a filling of the crescent-like blood sinuses bordering the gill bodies. A concomitant change in the shape of the branchial region is seen in connexion with contraction of striated branchial muscles. A. Resting phase. B. Early contraction and some twisting of the gill region. C. Maximal contraction with a broadening. D and E. Early and maximal stretching of the gill region.