

THE CIRCULATORY PHYSIOLOGY OF *HELIX POMATIA*
III. THE HYDROSTATIC PRESSURE CHANGES IN THE CIRCULATORY
SYSTEM OF LIVING *HELIX*

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INTRODUCTION

Most reports upon the circulatory physiology of molluscs have described results obtained with animals dissected to a greater or lesser extent and may have only limited significance for the intact animal. The present work has been concerned with measuring the changes in hydrostatic pressure in various parts of the circulatory system while interfering as little as possible with the normal activities of the animal.

The fluctuation in hydrostatic pressure has been studied in relation to variations in rate of heart beat and blood flow and to the mechanism of heart filling.

MATERIALS AND METHODS

The snails weighed 15-20 g each and were obtained from a biological supplier. Two instruments were used to measure pressure changes; firstly, a closed water manometer (Davson & Purvis, 1959) which deflected a light beam to a recording camera (Chadwick (Sommerville), 1962); secondly, a pressure transducer (Model P.23, B. B. Statham Inst. Inc., 254 Carpenter Road, Hato, Rey, Puerto Rico) used in conjunction with a 'Polygraph' pen recorder (Grass Instrument Co., 101 Old Colony Avenue, Quincy, Mass., U.S.A.).

The manometer and transducer were connected to the animal through leads of water-filled, 'rigid' Polythene tubing which terminated in an S 19 hypodermic needle (20 mm long; 0.3 mm bore). Ringer solution (Hedon-Fleig) was introduced into the needle and adjacent tubing.

During experiments the instruments were frequently calibrated against static changes in pressure to check that the response was linear and the base-line steady. Tests were carried out to determine the response of the Davson and Purvis manometer to dynamic pressure changes. The lowest vibration frequency was considered as the natural undamped frequency of the system. This was 31 c/s. An accuracy in the amplitude response of not more than 1% and not less than 5% could be expected up to a recording frequency of 0.69 c/s (McDonald, 1960). As this frequency is of the same order as the snail heart rate the pulse amplitude could be accurately recorded.

Heart rate and pressure recordings were carried out by inserting the hypodermic needle through Polythene windows which replaced the shell over appropriate areas. A window of approximately 1.5 cm square was sawn from the shell and a piece of heavy Polythene sheet was stretched to fit the shell curvature and fixed across the

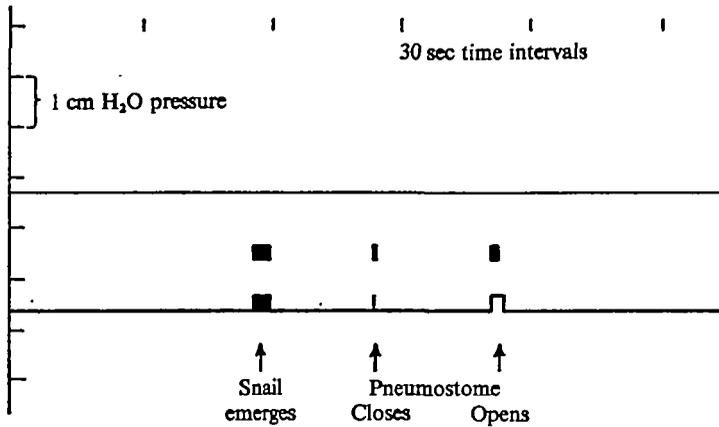


Fig. 1. Key to the marking of pressure recordings.

hole by sticking its border to the shell surrounding the window with 'UHU' adhesive.

Some recordings of the differential pressure between two parts of the circulatory system were made by connecting two Statham transducers so that the combined output was the difference in pressure recorded by each (Spencer, 1960).

EXPERIMENTS AND RESULTS

The diagrammatic cross-section of the snail (see fig. 1, Sommerville, 1973*a*) shows the relationship between the body cavities. During the breathing cycle the muscular floor of the mantle cavity (roof of the cephalopedal haemocoel) is depressed, increasing the volume of the cavity, the pneumostome opens and air enters. The pneumostome then closes and the mantle-cavity floor rises, reducing the volume of the cavity. This sequence of events is also associated with the extension of the head and foot from the shell (Sommerville, 1973*a*).

Although most pressure measurements were made by passing a hypodermic needle through a Polythene window into a selected part of the body, the measurements in the cephalopedal haemocoel were made through a 6 cm long, 1 mm bore Polythene cannula bearing 3-4 side holes near the open end. This was passed into the mouth of an extended animal and manoeuvred over the buccal mass to pierce the wall of the oesophagus and enter the haemocoel. The damage to the gut wall did not appear to affect the animals.

Variation in pressure with breathing movements

There are marked pressure changes associated with the movements of the floor of the mantle cavity and pneumostome. Although these changes are quite regular at any one position and time, the direction and magnitude of change can vary greatly.

(a) *Pressure in the cephalopaedal haemocoel*

There is always an increase in pressure while the pneumostome is open and usually a steady base-line while it is closed, although this pattern may be obscured

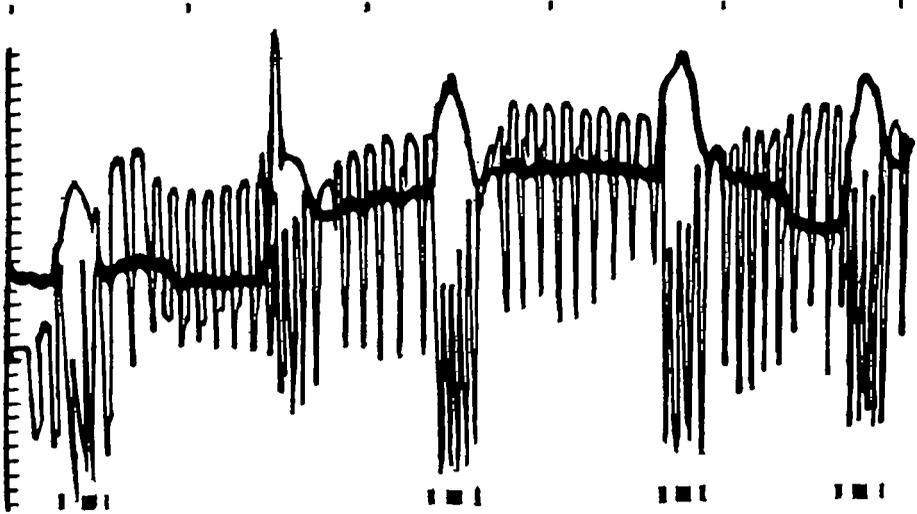


Fig. 2. Upper trace: pressure in cephalopedal haemocoel. Lower trace: pressure in ventricle. Initially inactive snail emerges from shell. Davson & Purvis manometer.

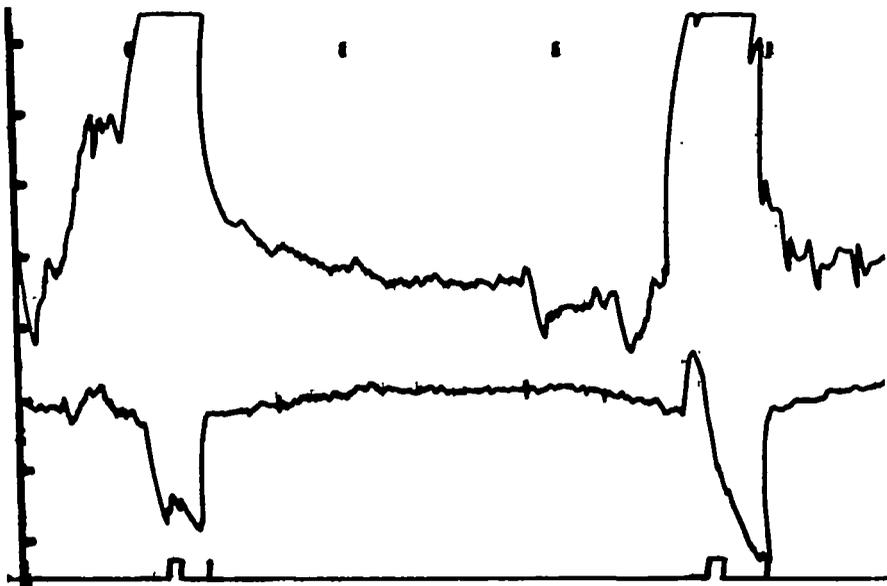


Fig. 3. Upper trace: pressure in large pulmonary vein near heart. Lower trace: pressure in small pulmonary vein far from heart. Snail fairly active. Statham transducer.

by the effects of general body movement. The upper trace in Fig. 2 shows pressure changes of 8 cm H₂O associated with the animal emerging.

(b) *Pressure in the mantle cavity*

The mantle-cavity pressure was measured by placing the needle either between the shell and the roof of the cavity or in a small pulmonary vein far from the heart.

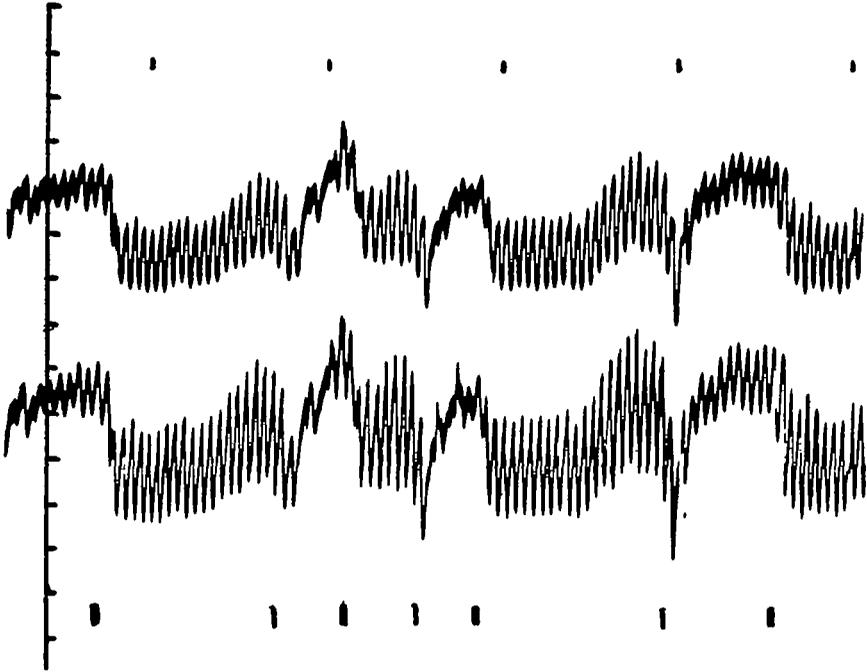


Fig. 4. Upper trace: pressure in pericardial cavity. Lower trace: pressure in large pulmonary vein near heart. Snail retracted. Davson & Purvis manometer.

The pressure always fell as the pneumostome opened and rose when it closed. The lower trace in Fig. 3 shows a typical pattern with a 2 cm H_2O pressure change.

(c) *Pressure in the pericardial cavity and heart*

A common pattern of pressure change related to the breathing cycle seen in the pericardial cavity consists of a rise and fall in the base line while the pneumostome is open and again while it is closed. The sequence of events shown in Fig. 4, recorded from a retracted animal, is as follows: (i) pneumostome opened, (ii) amplitude of heart-beat increased by a half, (iii) pressure increased gradually by 2 cm H_2O , (iv) pressure fell steeply, (v) pneumostome closed, (vi) pressure rose by 3 cm H_2O , (vii) base-line remained level with a low amplitude of heart beat, (viii) the pressure fell steeply by 3 cm H_2O .

Figs. 2 and 5 are recordings made from extended, active animals, showing a pressure rise in the ventricle (9 cm H_2O) and auricle (4 cm H_2O) while the pneumostome was closed and a fall in pressure while it was open.

Variation in pressure with other body movements

The beginning of the recording in Fig. 2 shows a general rise in blood pressure at the transition from an inactive to an active state. The basal pressure level in the cephalopedal haemocoel (upper trace) rose by 5 cm H_2O and in the ventricle by 11 cm H_2O . This recording also illustrates the distinctive pressure changes occurring in the body when the animal emerges from its shell. When the pneumostome was open, there was a rise and fall of 8 cm H_2O in the haemocoel and a corresponding fall

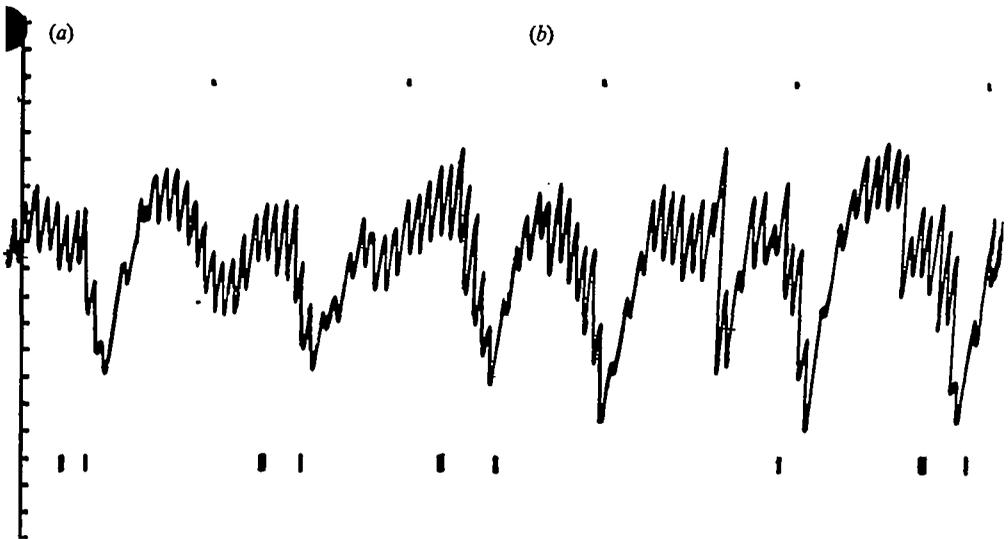


Fig. 5. (a) Pressure in auricle. (b) Pressure in large pulmonary vein near heart. Snail fairly active. Davson & Purvis manometer.

and rise in the ventricle of 9–12 cm H₂O as the animal emerged. While the pneumostome was closed, the animal remained still and the base-line remained level. A recording made of pericardial pressure has shown pressure peaks of up to 14 cm H₂O while the pneumostome was open and the animal was emerging. As soon as the animal was fully extended similar pressure peaks of about 5 cm H₂O occurred while the pneumostome was open and closed.

*The relationship between pressures measured simultaneously
in different parts of the body*

The relative position of the cephalopodal haemocoel and mantle cavity suggests that any movement of the muscle plate separating them could cause reciprocal pressure changes in the two cavities. This seems to be the case although the haemocoelic pressure may be complicated by other body movements. Fig. 6 shows the pressure changes in the two cavities during the breathing cycle. The contraction of the mantle cavity floor while the pneumostome was open increased the pressure in the cephalopodal haemocoel and increased the volume of the mantle cavity. When the pneumostome closed, the mantle-cavity floor rose, causing the pressure in the cephalopodal haemocoel to fall. The reduced volume of the mantle cavity resulted in an increased pressure there.

Since the heart lies at the back of the mantle cavity and rests on the roof of the cephalopodal haemocoel its basal pressure pattern is complicated. Fig. 3 shows a marked difference in the pressure patterns recorded simultaneously from the main pulmonary vein near the heart and a small pulmonary vein some distance away. The large vein showed an increased pressure while the pneumostome was open and the small vein a decreased pressure. The auricular pressure is usually very similar to that of the adjacent pulmonary vein (Fig. 5). The small pulmonary vein would be reflecting mantle cavity pressure.



Fig. 6. Upper trace: pressure in mantle cavity. Lower trace: pressure in cephalopedal haemocoel. Snail inactive. Davson & Purvis manometer.

Fig. 2 shows the mean ventricular pressure falling when the pneumostome was open, as if reflecting mantle-cavity pressure, while the cephalopedal haemocoel pressure rose. Fig. 4 illustrates a typical pressure pattern seen in the heart where the mean pressure level rose and fell while the pneumostome was open and again while it was closed apparently reflecting the peak pressures of both mantle cavity and cephalopedal haemocoel.

Variation in pressure with heart-beat

Fig. 4 shows the pressure changes occurring in the pericardial cavity associated with heart beat. The animal was inactive and the amplitude of beat on the trace represents 1.5 cm H₂O pressure change. In the active animal this may be as high as 7 cm H₂O. Fig. 7 shows that maximal pressure in the pericardial cavity corresponds with the lowest pressure in the ventricle, i.e. ventricular diastole. In pericardial cavity pressure recordings, auricular diastole is usually represented as a secondary peak superimposed on the ventricular diastolic wave as shown in the centre of Fig. 7 and in the lower trace of Fig. 8. This secondary peak is just visible on the upper trace in Fig. 4 but is missing from the otherwise similar lower trace which was recorded from the pulmonary vein. The close succession of auricular and ventricular diastolic pressure peaks recorded from the pericardial cavity is due to the rapid ventricular diastole of the *Helix* heart, but the peaks may be almost independent and the relative length of the auricular and ventricular cycle may vary with the breathing cycle. The lower trace in Fig. 8 shows the strict alternation of auricular and ventricular diastole, while the pneumostome is open, replaced by an irregular pattern of beat with long periods when both chambers are in diastole, while it is closed. Fig. 9 is a recording made from the pericardial cavity of *Archachatina purpurea* (the large African pulmonate) showing a pattern and magnitude of pressure changes associated with breathing movements and heart beat which is very similar to that of *Helix pomatia*.

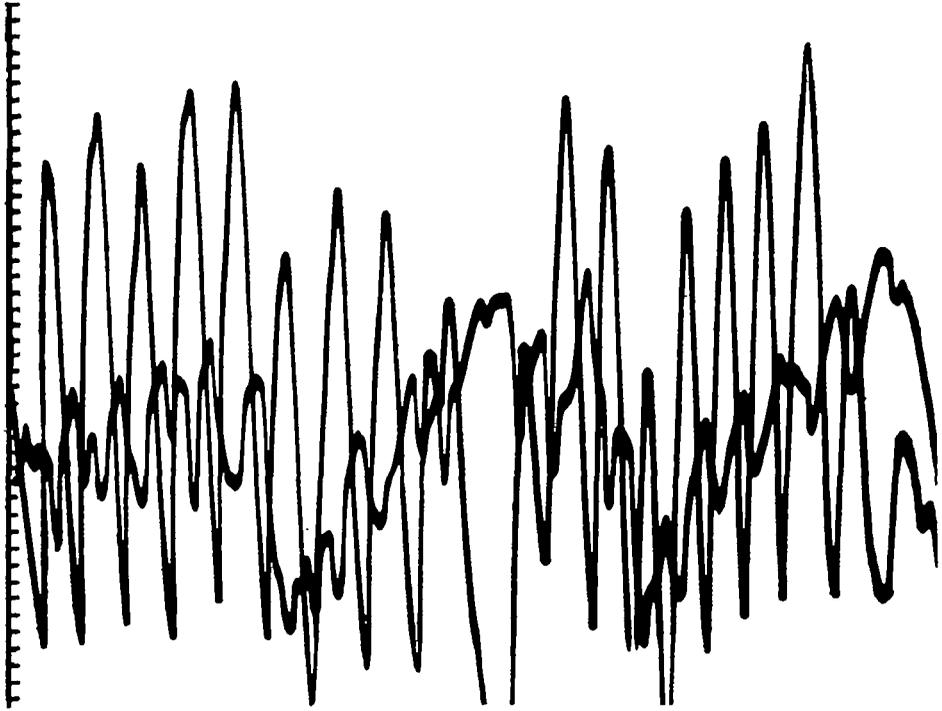


Fig. 7. Trace with large oscillation: pressure in ventricle. Trace with small oscillation: pressure in pericardial cavity. Snail inactive. Davson & Purvis manometer.

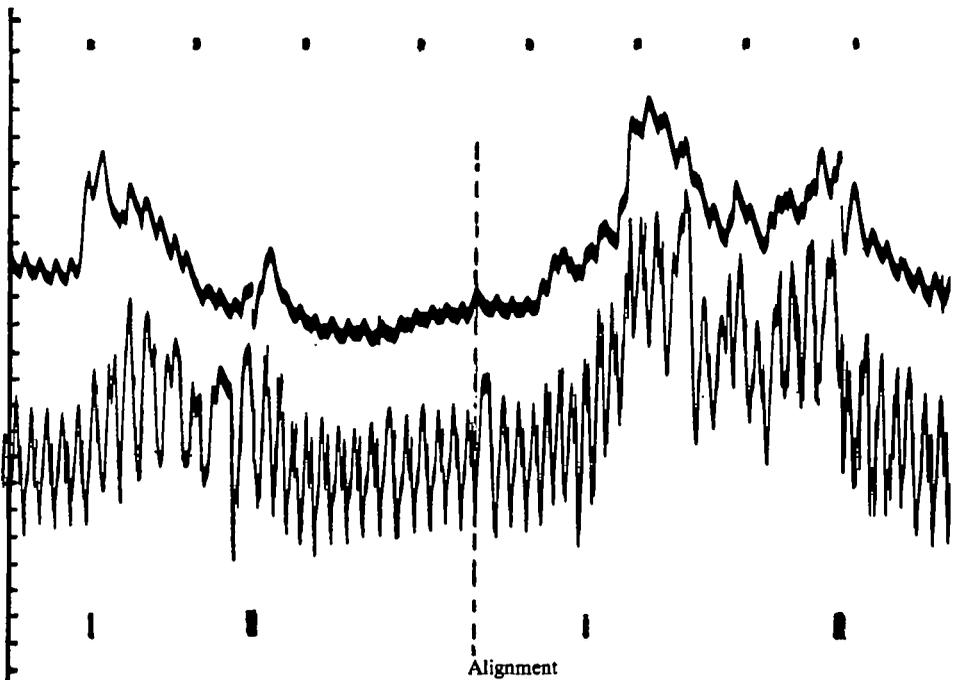


Fig. 8. Upper trace: pressure in cephalopedal haemocoel. Lower trace: pressure in pericardial cavity. Snail active. Davson & Purvis manometer.

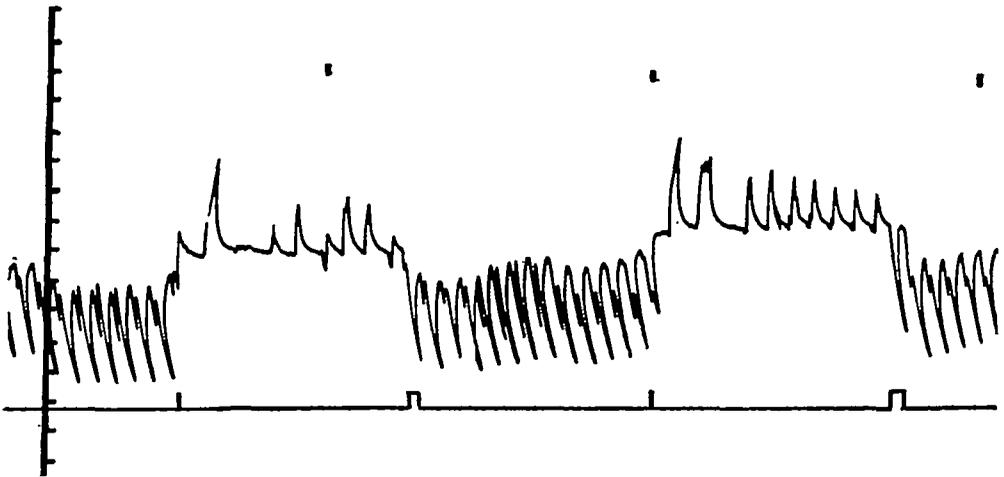


Fig. 9. Pressure in pericardial cavity. Snail (*Archachatina purpurea*) inactive. Statham transducer.

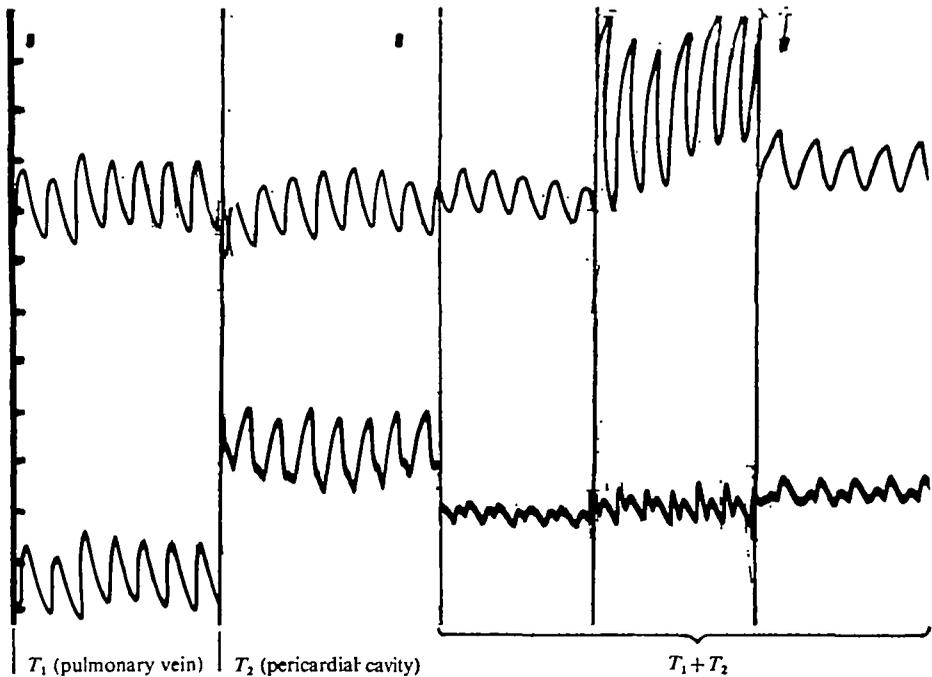


Fig. 10. Upper trace: pressure in large pulmonary vein far from heart. Lower trace: differential pressure between pulmonary vein near heart and pericardial cavity. Snail inactive. Statham transducers.

The difference between the diastolic and systolic pressure recorded within the ventricle varied from 10 to 32 cm H₂O (Figs. 2, 7).

The aortic pulse pressure change was 2-3 cm H₂O. The pulse wave had a flattened peak and sometimes showed a notch near the top of the descending limb.

Fig. 5 shows pressure recordings from the auricle and pulmonary vein which appear identical. The auricular pulse pressure change was 1.5 cm H₂O.

Fig. 8 shows that pulse waves can be recorded from the cephalopedal haemocoel. The peak pressure corresponds with ventricular systole (trough of pericardial cavity trace), indicating that the pulse has been transmitted by the aorta which passes through the cavity.

Differential pressure measurements

Since there is no veno-auricular valve present to restrict blood flow and since, during diastole, the thin-walled auricle is likely to be at the same pressure as the pericardial cavity, the differential pressure between pulmonary vein and pericardial cavity was measured to see whether a pressure gradient existed. The top trace in Fig. 10 shows a single transducer recording from the main pulmonary vein about 1.5 cm from the heart and, below, recordings from the paired transducers. The single recordings are labelled T_1 or T_2 and the differential recording is labelled $T_1 + T_2$. Transducer 2 (T_2) is recording increase in pressure as a downward movement so that troughs on the T_2 and $T_1 + T_2$ recordings indicate high pericardial pressure.

The differential recording shows that the pericardial pressure was lower than the pulmonary vein pressure at the peak of auricular systole and again at the beginning of auricular diastole. Assuming that the pericardial pressure closely resembles the auricular pressure at diastole, maximal blood flow would occur at the beginning of auricular diastole. The pressure gradient was 0.5–1 cm H₂O, a high amplitude of beat being associated with a high gradient.

This technique was used in an attempt to estimate the rate of blood flow. The theoretical foundation of the experiment was that the pressure recorded from the centre of a vessel with the open end of the manometer pointing against the flow would be greater than the pressure recorded with the open end pointing in the same direction as flow. The difference in pressure would be proportional to the rate of flow (Bernoulli's Theorem). The vessel chosen was the main pulmonary vein near the heart through which most of the circulating blood passes. Experiments carried out using Polythene tubing of appropriate bore (1.5 mm) instead of the pulmonary vein gave inconsistent measurements probably due to variation in the position of the needle ends relative to the wall of the tube, but a reasonable deflexion could be obtained with a flow rate of the order of 1 cc/min. Since conditions in the animal were so variable a calibration was carried out upon each preparation at the end of the experiment without disturbing the position of the needles. The two needles from the paired transducers were passed through a Polythene window into the cardiac end of the pulmonary vein, the needle nearest the heart pointing away from it and the other pointing towards the heart so that their tips lay 1 mm apart, 3–5 mm from the auricle. The output from a monitoring transducer, measuring pressure in a branch of the pulmonary vein, was recorded on the upper channel of the polygraph and the paired transducer output on the lower. By clamping off the recording lead of one of the pair, the single output from the other could be obtained and by clamping both, the zero output was found. A recording sequence of T_1 , T_2 , zero, $T_1 + T_2$ and zero was carried out to check the base-line levels and transducer performance. From time to time the balance of the paired transducers was tested.

Table 1. *Analysis of a recording made with three Statham transducers measuring the rate of blood flow by differential pressure*

Part of trace	Heart frequency (beats/min)	Amplitude of beat (mm of trace)	Area beneath monitoring pressure curve	Flow (displacement of differential base-line)	Area/Flow
<i>a</i>	29	3	5.88	8	0.7
<i>b</i>	26	11	14.09	15	0.9
<i>c</i>	30	10	14.04	25	0.6
<i>d</i>	31	15	18.39	35	0.5

The snail was retracted and inactive throughout and the increasing heart activity from 'a' to 'd' corresponded with recovery over a 20-min period following the insertion of the needles.

At the end of the experiment the monitoring transducer was replaced by a 100 cc syringe operated by a continuous slow injector (C. F. Palmer Ltd.) or a small-animal variable-stroke respirator pump (C. K. Palmer Ltd.) and saline was pumped through the preparation at different flow rates. The heart was cut across the atrio-ventricular junction to allow the fluid to escape. It was found that the calibration was the same whether the flow was steady or pulsatile.

Five experiments were carried out but the conditions proved so critical that a successful recording was never accompanied by a satisfactory calibration and vice versa.

Placing the needles in position usually depressed heart activity, but over the following 20–60 min the frequency and amplitude of beat rose steadily to the normal level. Table 1 shows the analysis of one experiment where a good correlation occurred between the increasing frequency and amplitude of beat and the increasing displacement of the ' $T_1 + T_2$ ' base-line. The size of the displacement bears a reasonably constant relationship to the area beneath the monitoring pressure curve, which provided an independent measure of flow rate.

DISCUSSION

The pressure relationships of the heart and pericardial cavity are complicated. The intracardial pressure is affected by the pressure in the pulmonary vein and aorta and these may be affected by the pressures in the mantle cavity and/or haemocoels. The pericardial pressure is dependent on the degree of filling of the heart and may be directly affected by the haemocoelic and/or mantle-cavity pressure.

The mean heart pressure can vary by up to 9 cm H₂O during the breathing cycle and this may have some relation to the changes in heart activity noted, although the overriding control of consistent heart changes associated with the breathing cycle appears to be nervous (Sommerville, 1973*a*).

The absence of a veno-auricular valve in the molluscan heart (with the exception of the cephalopods) has prompted various authors to look for some mechanism to limit the backflow of blood at auricular systole. Nalepa (1883) stated that the pulmonary vein of *Zonites* contracted at the same time as the auricle and Brucke (1925) claimed this for *Helix*. This has not been observed during the present work – in fact, the vein dilates at auricular systole. This could be accounted for either by an obstruction to flow due to occlusion of the veno-auricular opening, or by a backflow

of blood from auricle to vein. Schwartzkopff (1954) maintained that the muscular protuberances in the auricle near its junction with the vein separated the two parts during auricular systole. The vertebrate heart is built on a similar plan to that of *Helix*, and in those vertebrates with a pulmonary circulation there is no valve between the pulmonary vein and auricle. This is probably because the pulmonary venous system is short and back pressure builds up quickly. This could also apply to the molluscan arrangement.

Another subject for conjecture is the role played by the pericardium in the physiology of the molluscan heart. It seems generally accepted that one of its main functions is to prevent over-distension since the direct relationship between the power of contraction and the distension of a muscular chamber only holds up to a certain limit (Batham & Pantin, 1950).

Türk-Meiningen (1934) noted that the heart of *Helix* retained its co-ordination only if the pericardial wall was under tension. Schwartzkopff (1954) proposed that co-ordination depended upon the distal ends of the two heart chambers being anchored at opposite sides of the pericardial cavity so that the contraction of one chamber would stretch the other and lower its threshold for contraction.

The obvious explanation of filling is to postulate a pressure gradient from the pulmonary vein to the auricle and ventricle (Bieirng, 1929; von Skramlik, 1941; Schwartzkopff, 1954). Jullien & Ripplinger (1953) state that the pulmonary vein pressure varies from 2 to 10 cm H₂O. Measurements made during the course of this work confirm this range, the highest pressure recorded being 11 cm H₂O above atmospheric pressure. The volume-compensation-chamber theory to account for co-ordination and filling of the molluscan heart chambers has been put forward by Willem & Minne (1898), von Skramlik (1941), Ramsay (1952), Krijgsman & Divaris (1955), Jones (1971) and Civil & Thompson (1972). This theory rests upon the assumptions that, firstly, the pericardium is functionally rigid and, secondly, the pericardial cavity is functionally sealed. The pericardial cavity would then be of constant volume and contraction of one heart chamber would induce dilation of the other in strict alternation. Von Skramlik proposed this mechanism to account for the filling of the lamellibranch heart and Brand (1972) confirmed this in *Anodonta anatina* despite the large reno-pericardial opening present.

Jones (1971) measured the absolute pressures in the auricle, ventricle and pericardial cavity of live *Helix*. The figures reported here (except those of the mantle cavity) are pressure changes and their relationship to atmospheric is not known, so direct comparison with those of Jones can only be made for pulse pressures and the average values for an inactive animal agree closely with his. Jones states that the pericardium is 'kept rigid' by the slight pressure (1–3 cm H₂O) of the pericardial fluid in excess of atmospheric pressure, thus allowing the volume-compensation arrangement to fill the heart chambers. However, this situation could not be maintained when the pneumostome closes since the mantle cavity pressure then rises to between 1 and 8 cm H₂O above atmospheric pressure.

Civil & Thompson (1972) have shown that the isolated heart will only pump fluid if it is surrounded by a rigid, sealed chamber, but Schwartzkopff (1954) and Sommerville (1973*b*) have shown that efficient pumping occurs without a pericardium, providing the first aortic valve (Sommerville, 1973*a*) is included in the preparation.

By watching the heart of *Helix* beating in its normal relationship with the surrounding organs it is seen that the walls of the pericardium are not functionally rigid and the total volume of auricle and ventricle can vary considerably. Neither do the two heart chambers contract and expand in strict alternation as the pressure recordings made during this work show. However, the contraction of the ventricle does cause a fall in pericardial pressure, and differential pressure measurements made between the pericardial cavity and pulmonary vein show that there is a pressure gradient tending to fill the auricle at the beginning of its diastole. In so far as the contraction of the ventricle contributes to this gradient, possibly due to a lag in the deformation of the pericardium, there is some support for the volume-compensation-chamber hypothesis, but this contribution is probably boosted by a relatively high venous pressure.

Biering and von Skramlik postulated that the ventricle generated a sufficiently high blood pressure to maintain a gradient from vein to auricle. The present work indicates that in the active animal such a source of pressure would be insignificant compared with the pressure generated by body movement. Türk-Meiningen (1934) found that inflating the lung through a tube ligatured into the pneumostome resulted in an increased heart rate. Jullien & Ripplinger (1953) observed that when the floor of the mantle cavity was depressed, particles of Chinese ink injected into the haemocoels passed into the veins afferent to the lung and on into the efferent pulmonary veins, where an increase in pressure was recorded. When the floor of the mantle cavity was raised the particles passed back from the efferent to the afferent veins and a drop in venous pressure occurred. They also noted the variation in heart volume associated with the breathing cycle and attributed it to an increased blood supply with the lung floor acting as a peripheral heart. The present work provides evidence to support this suggestion in that there are reciprocal pressure changes in mantle cavity and cephalopodal haemocoel and that increased venous return (pressure) results in an increased frequency of beat in the isolated heart (Sommerville, 1973*b*), but a consistent direction of change in frequency of beat only seems to occur in an animal with intact cardiac nerves (Sommerville, 1973*a*). The present work has also shown that an increase in frequency and amplitude of heart beat was associated with an increased rate of flow, but it is uncertain whether the change in blood flow was the cause or the effect of the change in heart activity.

SUMMARY

1. The pressure changes in the mantle cavity and various parts of the circulatory system of *Helix pomatia* have been measured.
2. There are characteristic pressure changes associated with the breathing movements, the pattern depending upon the point at which the measurement was made and, in the case of the heart, the position of the body at the time of recording. These pressure changes fall mainly within the range 2–8 cm H₂O.
3. The pressure changes associated with contraction of the heart chambers fall within the range 1–2 cm H₂O in pulmonary vein and auricle, 10–32 cm H₂O in the ventricle, 1–3 cm H₂O in the aorta and 1–8 cm H₂O in the pericardial cavity.
4. An increased frequency and amplitude of heart beat was associated with an increased rate of blood flow.

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