

BLOOD PRESSURE AND ITS HYDRAULIC FUNCTIONS IN *HELIX POMATIA* L.

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(Received 19 March 1973)

INTRODUCTION

A hydrostatic skeleton has been defined as a liquid mechanism which, in one way or another, provides a means by which contractile elements can be antagonized (Chapman, 1958). Studies on the hydrostatic skeleton of soft-bodied invertebrates have been carried out by numerous authors – Chapman (1950) on worms, Batham & Pantin (1950*a*) on *Metridium*, Trueman (1966, 1967) on bivalves, Trueman & Ansell (1968) on *Peachia*, Trueman & Goodbody (1969) on *Ascidia* and more recently Seymour (1969, 1970, 1971) on annelids. All the above are animals of a basic cylindrical shape involving two sets of muscles, usually circular and longitudinal, with an antagonizing liquid ranging from the contents of the enteron to coelomic fluid.

In the pulmonates the true coelom comprises only the pericardial, nephridial and gonadal cavities and is not skeletal (Lankester, 1893); the general body cavity is haemocoelic and the muscle-antagonizing agent is the blood. It is necessary therefore, for an understanding of the hydraulic skeleton of pulmonates, to be familiar with the pattern of the vascular system. Grassé (1948), Hyman (1967) and Morton (1967) provide general accounts of pulmonate circulatory systems, whilst Bullough (1950), Borradaile *et al.* (1963), Ripplinger (1957) and Potts (1967) give accounts of isolated parts of the vascular system. Schmidt (1916) provides a thorough account of the vascular system of *Helix pomatia*, but unfortunately his and the above works lack detail essential to the following study.

The use of the vascular system of pulmonates as a hydraulic mechanism is not well documented. Morton (1967) suggests two skeletal functions of blood pressure in pulmonates – erection of optic tentacles and opposition of locomotory waves. Jones (1970) maintains that hydrostatic pressure in *Helix pomatia* is necessary for the erection and the maintenance in an erect condition, of the tentacles and the shell and viscera. Jones (1973, in preparation) suggests, in slugs at least, that haemocoelic pressure is necessary for the depression of pedal waves, whilst Meisenheimer (1912) and Runham & Hunter (1970) consider that the penis of pulmonates is everted by blood pressure.

The purpose of these experiments was to measure pressures in all accessible parts of the haemocoel of a representative terrestrial pulmonate *Helix pomatia* and to evaluate the significance of these pressures as muscle-antagonistic forces. As the vascular system is adapted to form a hydraulic mechanism it was necessary to carry out basic anatomical studies.

Anatomical

MATERIALS AND METHODS

Adult *Helix pomatia* were relaxed overnight in a 1% solution of propylene phenoxytol. After relaxation a hole was cut in the shell, dorsal to the pericardium, using a dental burr. To display the arterial system coloured latex solution (Phillip Harris Ltd) was injected directly into the ventricle; for the venous system latex was injected into the auricle. Latex was also injected into the cephalopedal sinus, visceral sinus and general haemocoel of the foot to determine the extent and relationship of the collecting vessels. Unfortunately, when an animal is narcotized by the above method, swelling of the haemocoelic spaces of the foot, caused by osmotic influx, occludes the pedal veins. Quick freezing of extended animals in liquid nitrogen followed by 'steak' sectioning was the technique found most satisfactory for display of these collecting veins. In order to study flow, methylene blue in saline was injected into various parts of the haemocoel, its final destination being noted.

Continuous pressure recording

Pressures were recorded using a Statham P23.BB pressure transducer coupled to a linear pen recorder (Narco Bio-Systems Inc.). Flexible Polythene tubing was used to connect the transducer to a 16-gauge hypodermic needle which was held in a Narishige manipulator. Where possible, synchronous recordings of pressure from two or more parts of the haemocoel were attempted, but not always successfully. To record heart pressures an area around the heart was exposed by drilling a small hole with a spherical dental burr and prising away the shell with a scalpel blade. The hypodermic needle could then be manipulated into the desired position. The pressure in the visceral sinus was recorded in a similar manner. To record cephalopedal sinus pressure flexible Polythene tubing of external diameter 1.4 mm and bore 0.8 mm was used. A series of holes were drilled in the end which entered the animal to avoid complete occlusion by the viscera. The animal was allowed to extend and was then held by its stalk whilst the tube was pushed gently but swiftly up the buccal mass until it penetrated the gut wall and lay in the cephalopedal sinus.

The experimental animal was fixed by its shell in a burette clamp. After each recording the transducer was calibrated against a known head of water. All pressure recordings were made in air at room temperature and are calibrated in centimetres of water.

Indirect pressure determinations

A direct manometric technique was employed to determine the pressure required to erect the optic tentacles of *Helix pomatia*. Adult specimens were relaxed overnight in a 1% solution of propylene phenoxytol. The optic tentacle with an area of surrounding skin was removed with a scalpel and the tentacular retractor muscle was removed. The base of the tentacle was tightly secured with a thread to a hypodermic needle which was connected to a manometer tube. The arrangement was such that a head of water could be applied to the tentacle to bring about its erection, and this pressure was read off the manometer scale.

When extended the shell and viscera are supported on the dorsal side of the foot by the pressure of the blood in the stalk. The stalk is a blood-filled cavity, continuous

Table 1. *The sequence of arteries which branch from the aorta as it passes anteriorly, and their ultimate destination*

(The renal artery subdivides into several major branches only two of which actually supply the kidney. Note that the posterior aorta is the only vessel supplying blood to the viscera, all other vessels terminating in the foot, head or stalk. Nomenclature after Schmidt, 1916.)

Artery	Ultimate destination
Pericardial	Heart
Renal:	
Intestinal	Crop
Albumen	Albumen gland
Uterine minor	Spermooviduct
Rectal	Rectum
Dorsal renal	Kidney
Ventral renal	Kidney
Seminal receptacle	Seminal receptacle
Major uterine	Spermooviduct, dart sac, vas deferens, vagina
Salivary	Salivary glands, crop, oesophagus, dorsal pharyngeal muscles
Posterior parietal	Columella muscle, and body wall
Posterior circumpallial	Posterior edge of mantle
Anterior circumpallial	Anterior edge of the mantle
Pedal	All regions of the foot
Buccal	Radula sac and buccal bulb
Cephalic (right and left)	Tentacles, penis, flagellum, genital orifice, body wall

with the cephalopedal sinus, which joins the visceral mass to the foot. The pressure of the blood in the stalk must be at least equal to the downward force of the shell and viscera to prevent collapse of the sinus. This force was calculated by dividing the wet weight of the shell and viscera by the area of the stalk and expressed in g/cm^2 .

RESULTS

Anatomy of the vascular system

The two-chambered heart, enclosed in a pericardial sac, is bounded on one side by the nephridium and on the other side by the mantle cavity. The thin-walled auricle opens via a pair of valves into the more muscular ventricle (Chadwick, 1962). A valve at the apex of the ventricle prevents backflow of blood at ventricular diastole. A second aortic valve, further down the aorta, may serve to limit arterial resistance to the pressure of the visceral sinus rather than of the cephalopedal sinus (Chadwick, 1962).

The arterial system. The aorta, after leaving the ventricle, splits almost immediately into a visceral branch (posterior aorta) passing along the ventral surface of the digestive gland to the general viscera, and a cephalic branch (anterior aorta) which passes anteriorly, through the cephalopedal sinus, to supply the head and foot. Table 1 shows the sequence of arteries arising from the aorta after leaving the ventricle and the destination of these arteries.

The venous system. There is no distinct capillary system in pulmonates; a system of fine branching arteries and subsequently small lacunal spaces ensures an adequate supply of blood to all tissues. Blood drains from the lacunal spaces into larger central haemocoelic spaces. Blood in the viscera ultimately collects in the visceral sinus, whilst blood from the anterior region of the animal collects in the large cephalopedal sinus. Fig. 1 is a diagrammatic representation of the venous system of *Helix pomatia* to show the spatial relationship of the collecting sinuses to the circulus venosus.

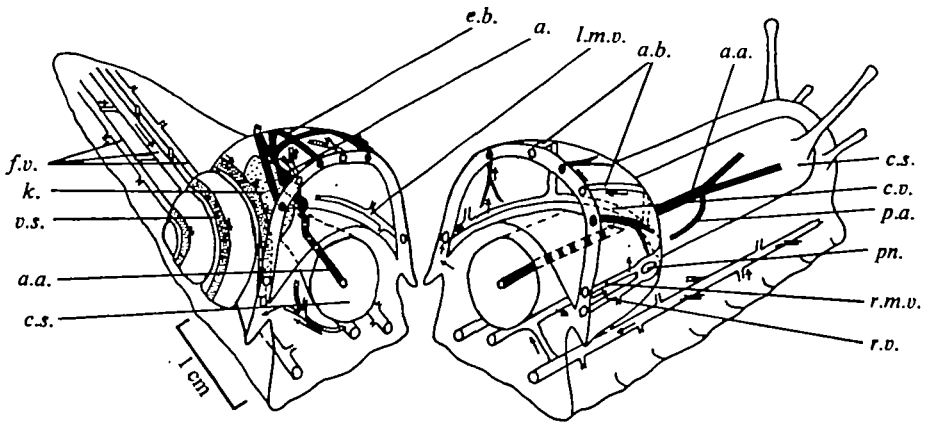


Fig. 1. A diagrammatic representation of the venous system of *Helix pomatia* to show the relationship of the collecting vessels to the circulus venosus (see text for full explanation). The efferent branchial vessels, the heart and the anterior aorta are shown in black, whilst the kidney (indicating the position of the sub-renal sinus) and the visceral sinus are stippled. The direction of blood flow is indicated by arrows. *a.*, Auricle; *a.a.*, anterior aorta; *a.b.*, afferent branchial vessels; *c.s.*, cephalopedal sinus; *c.v.*, circular vein; *e.b.*, efferent branchial vessels; *f.v.*, foot vein; *k.*, kidney; *l.m.v.*, left marginal vein; *p.a.*, pedal artery; *pn.*, pneumostome; *r.m.v.*, right marginal vein; *r.v.*, rectal vein; *v.s.*, visceral sinus.

The foot of *Helix pomatia* is composed of muscle fibres orientated in several directions with small haemocoelic spaces between the muscles. Blood is distributed to all parts of the foot by the large pedal artery and its branches, and eventually flows into one of the three pedal collecting veins. Two are laterally placed and one, the median foot vein, lies above the mucus gland. All three are interconnected and lie longitudinally along the length of the foot. The median vein is connected via a duct to lacunal spaces on the right side of the diaphragm (Grassé, 1948). Situated between the visceral sinus and the cephalopedal sinus is a smaller sinus, the sub-renal, which lies beneath the kidney and above the digestive gland. Blood in the cephalopedal sinus is partially separated from blood in the sub-renal sinus by an incomplete septum.

Blood in the large spaces eventually reaches the lung via the circulus venosus (after Schmidt, 1916). This is a ring of marginal vessels around the edge of the lung consisting of

- (1) The right marginal vein, which drains blood from the viscera and passes along the right edge of the mantle.
- (2) The circular vein, part of which forms the annular ring around the pneumostome and joins the left marginal vein to the right marginal vein.
- (3) The left marginal vein, which extends along the left side of the mantle.
- (4) The rectal vein, which drains blood from the sub-renal sinus and runs along the right side of the animal below the right marginal vein.

The circulus venosus constitutes the afferent branchial system whilst a system of efferent branchial vessels transports oxygenated blood to the auricle. The kidney receives blood from the sub-renal sinus and the right marginal vein together with a direct arterial supply. Fig. 2 summarizes blood flow in *Helix pomatia*.

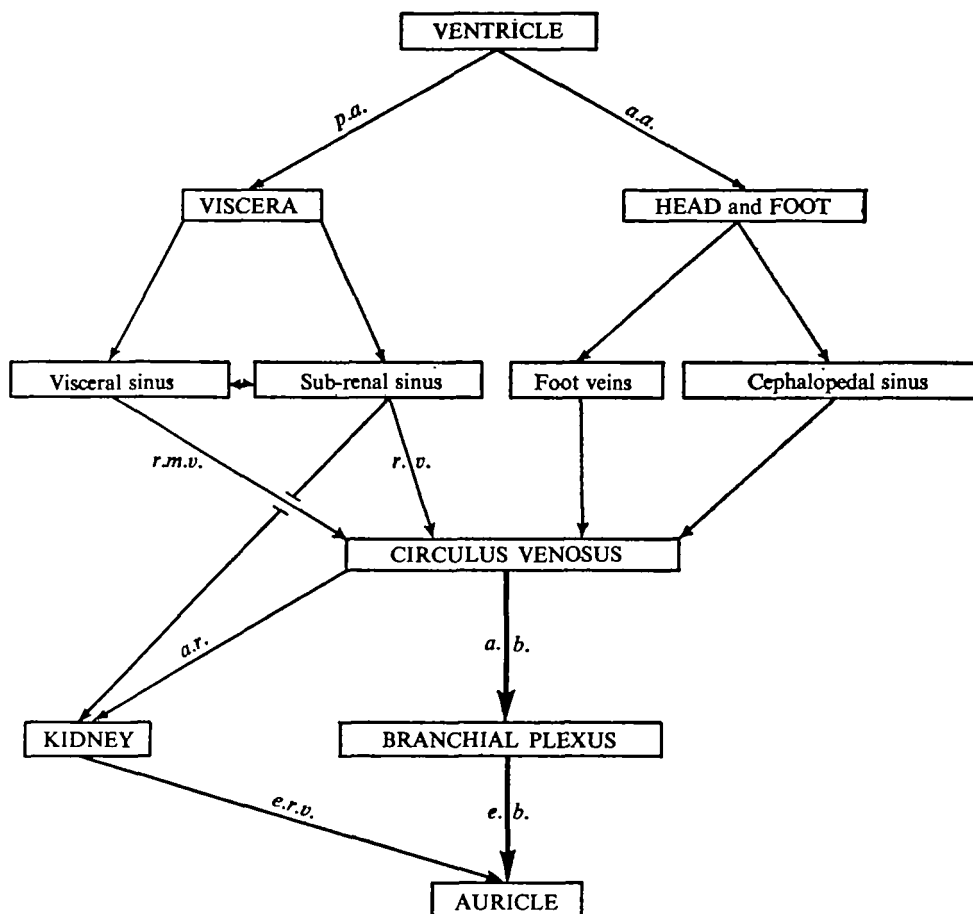


Fig. 2. A diagram summarizing blood flow in *Helix pomatia*. The kidney receives blood from the sub-renal sinus and the afferent renal vessels (those branches of the right marginal vein proximal to the kidney). The remaining branches of the right marginal vein constituting part of the afferent branchial system. *a.a.*, Anterior aorta; *a.b.*, afferent branchial vessels; *a.r.*, afferent renal vessels; *e.b.*, efferent branchial vessels; *e.r.v.*, efferent renal vein; *p.a.*, posterior aorta; *r.v.*, rectal vein; *r.m.v.*, right marginal vein.

Continuous pressure recordings

Ventricular systolic pressure ranges from 20 to 35 cm, depending upon the state of activity of the animal (Fig. 3). Traces (a), (b) and (c) are pressure recordings from the ventricle of animals which, prior to recording, could be considered as normal, active animals. Such recordings show characteristically high systolic pressures of up to 35 cm and a high frequency of beat up to 60 beats/min. Trace (d) is from an animal again extended but which, prior to recording, was in a state of hibernation. The epiphragm was removed immediately before recording. In this case systolic pressure is significantly lower, being about 20 cm, and the frequency is correspondingly lower – about 20 beats/min. Diastolic pressure, however, appears to be independent of activity, having a value of 4–6 cm.

Cephalopedal sinus pressure varies from 10 to 25 cm, again depending upon the

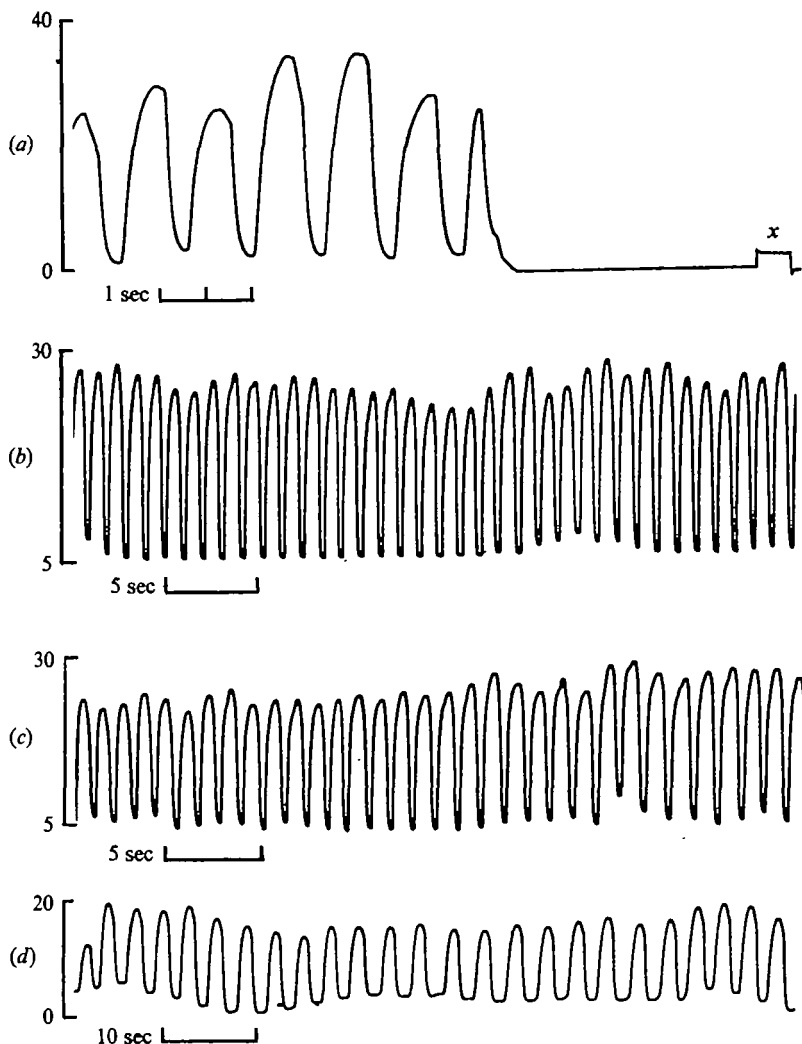


Fig. 3. Pressure recordings from the ventricle of *Helix pomatia*. (a), (b) and (c) are from active, extended animals whilst (d) is from an animal which, prior to recording, was in a state of hibernation. (x) is a calibration deflexion equivalent to 2.5 cm of water. All these and subsequent pressure recordings are in centimetres of water.

state of activity of the individual animal (Fig. 4). The average pressure in the cephalopodal sinus of an extended but inactive animal is between 14 and 16 cm. Stimulation, by pinching the optic tentacles, causes retraction of the animal and an increase in blood pressure in this sinus of about 6 cm (Fig. 4a). Fig. 4(b) is a synchronous recording of pressure from the cephalopodal sinus (above) and the ventricle (below). Periodic decreases in blood pressure in the cephalopodal sinus are a result of repeated elevation of the muscular floor of the mantle cavity increasing the volume of this sinus.

Visceral sinus pressure is easier to record and does not fluctuate as does cephalopodal sinus pressure. The average pressure in this sinus is between 8 and 10 cm.

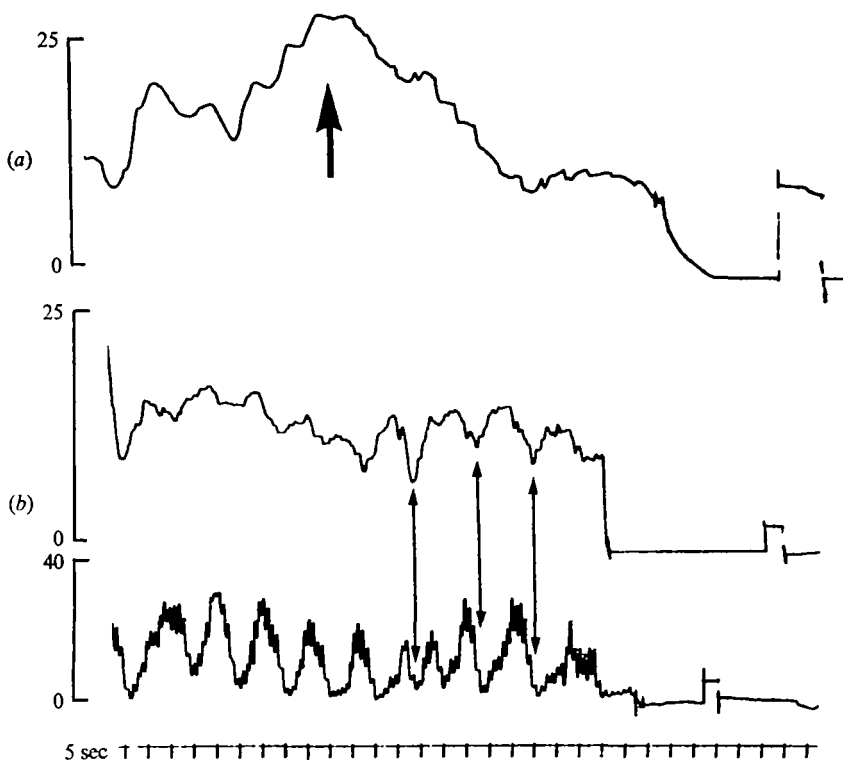


Fig. 4. (a) Pressure recording from the cephalopedal sinus of *Helix pomatia* showing the effect of retraction of the head (arrowed). (b) Synchronous pressure recording from the cephalopedal sinus (above) and ventricle (below), showing the effect of respiratory movements (arrowed). Zero pressures are recorded on all traces.

(Fig. 5). Fig. 5(a) shows the effect of forced retraction on pressure within the cephalopedal and visceral sinuses. On retraction cephalopedal sinus pressure increases by about 6 cm whilst pressure in the visceral sinus increases by 2–4 cm. On extension of the animal there is a gradual decrease in visceral sinus pressure by about 2 cm (Fig. 5b).

Venous blood returns to the auricle at a pressure of approximately 5 cm (Fig. 6). Traces (a), (b) and (c) are recorded from extended yet inactive animals showing that the pulse pressure in the auricle is barely 1 cm – just sufficient to exceed pressure in the relaxed ventricle and so completing the circulation. Fig. 6(d) is a synchronous recording of pressure from the ventricle (above) and the auricle (below) of a hibernating animal with the epiphragm intact, showing that the circulatory gradient, between the aorta and the pulmonary vein, is only 15 cm in an inactive animal.

Indirect pressure determinations

Using the manometric technique described, the mean pressure required to erect the isolated optic tentacle of an adult *Helix pomatia* is 16 cm.

In the extended animal the mean force exerted by the shell and viscera on the stalk was calculated as 8 g/cm². Blood pressure in the cephalopedal sinus must exceed this

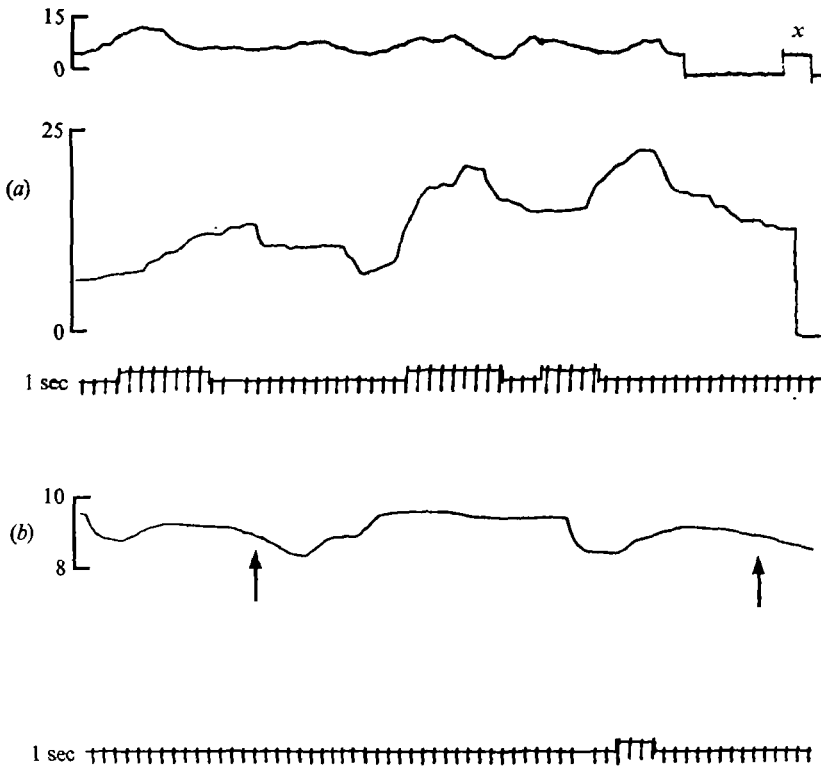


Fig. 5. (a) Synchronous recording of pressure from the visceral sinus (above) and cephalopedal sinus (below) of *Helix pomatia*. Event marks indicate a period of stimulation; (x) is a calibration deflexion equivalent to 6.25 cm of water. (b) Pressure recording from the visceral sinus of *Helix pomatia* showing the pressure decrease during extension of the head/foot (arrowed).

value to prevent constriction of various organs, such as the alimentary canal, when the animal is extended. Furthermore, blood in the lacunal spaces and veins in the region of the stalk must be at a pressure exceeding 8 cm to be able to flow.

DISCUSSION

Fig. 7 is a diagram of the vascular system of *Helix pomatia* to show the degradation in blood pressure from the arterial side of the heart to the venous side. Blood is pumped into the aorta at a pressure ranging from 20 to 35 cm of water and can flow either to the head and foot via the anterior aorta, or to the viscera via the posterior aorta. Blood drains from the visceral organs into the visceral sinus at a pressure of 8–10 cm, whilst blood in the anterior region of the animal collects in the large cephalopedal sinus at a pressure of 15 cm. All venous blood ultimately drains into the circulus venosus, a ring of veins around the base of the visceral mass. Although it was not possible to measure blood pressure in these veins, it was estimated, using the following argument, as being in the order of 8 cm. The viscera and shell exert a force on the stalk of 8 g/cm²; in order to flow, the venous blood of this region must be at a pressure exceeding this value. Furthermore, as blood flows directly from the visceral sinus into the right marginal vein and the pressure in the visceral sinus is between

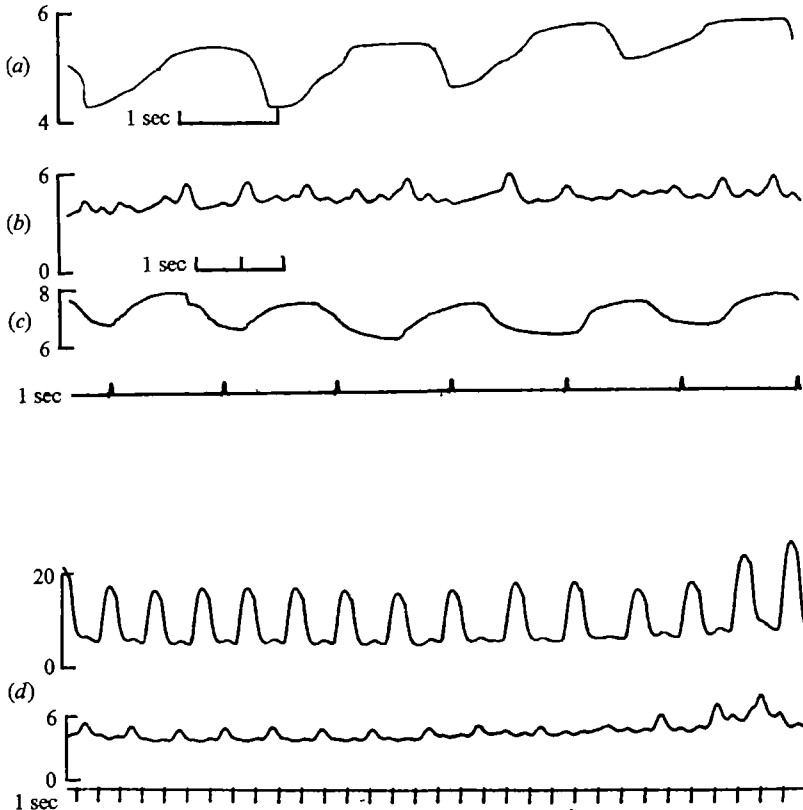


Fig. 6. Traces (a), (b) and (c) are pressure recordings from the auricle of *Helix pomatia* showing that venous return pressure is about 5 cm of water. (d) is a synchronous recording of pressure from the ventricle (above) and auricle (below) of an animal which prior to recording was in a state of hibernation. Note the decreased amplitude and frequency of ventricular beat.

8 and 10 cm, then the pressure in this vein must be at maximum 10 cm. From the circulus venosus blood flows through the branchial plexus at a pressure of 5–8 cm and returns to the auricle at 5 cm. A proportion of venous blood passes through the renal plexus (Fig. 2) and returns to the auricle via the renal vein. Blood pressure in this plexus is difficult to determine but at minimum it will be between 5 and 8 cm. There is evidence to suggest that ultrafiltration of the blood of *Helix pomatia* occurs through the walls of these renal veins (Vorwohl, 1961); if this is the case, by an arrangement such as found in the mammalian glomerulus, blood pressure could possibly be quite high at the actual site of filtration. Owing to the difficulties in measuring pressure in the haemocoelic spaces of the foot, the following approximations were made. Blood reaches the small sinuses of the foot by the pedal artery and its branches (Table 1). As this vessel passes along the floor of the cephalopedal sinus the blood inside, in order to flow, must be at a pressure exceeding that of the surrounding blood (15 cm). Blood ultimately collects in one of the three pedal collecting veins and then flows into the lacunal spaces on the right side of the diaphragm (Fig. 1). From these spaces blood flows into the circulus venosus where, as has previously been shown, the pressure is 8 cm. Consequently the pressure in the haemocoelic spaces of the foot will be between 8 and 16 cm.

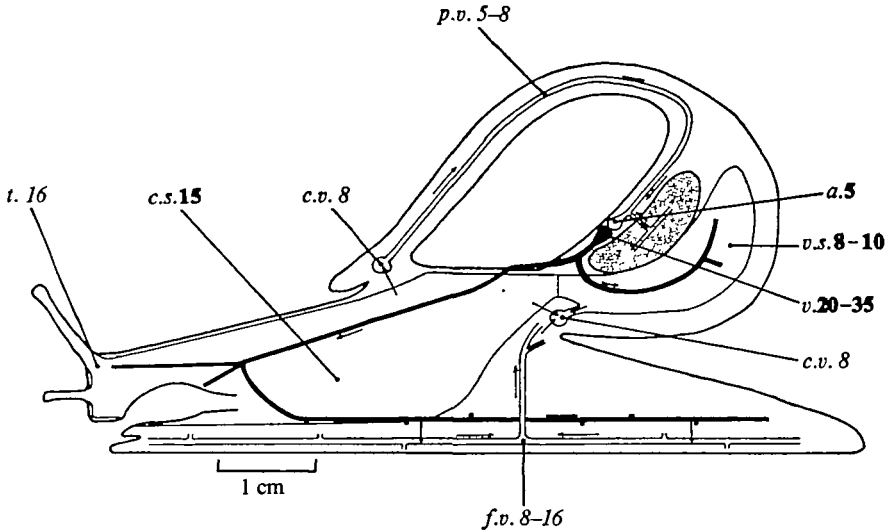


Fig. 7. A diagrammatic representation of the vascular system of *Helix pomatia* to show the degradation in blood pressure from the arterial end to the venous end of the heart. The direction of blood flow is indicated by arrows. The ventricle and the main arteries are shown in black whilst the kidney is stippled. Blood pressure, in cm of water, measured directly in several parts of the haemocoel is indicated in bold figures, whilst estimated values of pressure for the inaccessible parts of the haemocoel are indicated in italics. *a.*, Auricle; *c.s.*, cephalopedal sinus; *c.v.*, circulus venosus; *f.v.*, foot vein; *p.v.*, pulmonary vein; *t.*, tentacle; *v.*, ventricle; *v.s.*, visceral sinus.

The above figures for *Helix* blood pressure are similar to those obtained by previous authors. Jullien & Ripplinger (1953) measured the pressure in the pulmonary vein of *Helix pomatia* and obtained values between 2 and 8 cm, whilst Schwartzkopff (1954) estimates, from his results on isolated *Helix* heart, that the pressure in the aorta may reach 35 cm. More recently Jones (1971) measured the systolic pressure of the ventricle of a resting *Helix pomatia* as 24 cm and the diastolic pressure in the auricle as 5 cm.

The pressure of the blood in the circulus venosus has been estimated as being in the order of 8 cm, this being adequate (1) to overcome the resistance presented by the vessels of the branchial plexus and subsequently flow into the relaxed auricle at a pressure of 5 cm, (2) to effect the process of ultrafiltration at the renal plexus.

As shown previously, blood flows into the circulus venosus from four main vessels, namely the visceral, sub-renal, and cephalopedal sinuses and the foot veins (Fig. 2). Blood in the first two sinuses flows directly into the circulus venosus; is of the same order of pressure as circulus venosus blood; has no apparent hydrostatic functions and thus need only flow to the auricle. Blood in the latter sinuses has to flow through a system of lacunal spaces before entering the circulus venosus (therefore is comparatively isolated), is of a much higher pressure than circulus venosus blood, and has obvious hydrostatic functions.

Morton (1967) and Jones (1970) suggest that blood pressure is necessary for erection of the tentacles. A pressure of approximately 16 cm is required to erect the isolated optic tentacle of an adult *Helix pomatia* and this is within the range of pressure measured in the cephalopedal sinus of live animals. Both pairs of tentacles are erected

by the pressure of the blood in the cephalopedal sinus. Each tentacle has a retractor muscle, attached to its tip, which branches off the main columella muscle in the region of the stalk. Each muscle passes through a septal sheath, proximal to the tentacle, which serves to hold a quantity of blood solely for tentacle erection. This arrangement enables the tentacles to be erected, maintained in a vertical position and retracted independently of other body movements. Blood pressure in the stalk serves to support the shell and viscera (when the animal is extended) midway along the length of the foot and thus allows normal physiological processes to continue in this region.

The columella muscle, in the region of the stalk, divides into numerous branches all antagonized by the pressure of the blood in the cephalopedal sinus. The main central mass of muscle is inserted on to the sole of the foot and serves to erect the shell and viscera on to the back of the animal. The anterior pedal retractor muscles and the posterior pedal retractor muscles, on contraction, withdraw the animal into its shell. These muscles are returned to their normal length by blood pressure, but protrusion of the retracted animal is achieved mainly by forced respiratory movements. When the muscular floor of the mantle cavity contracts, the floor is lowered, causing an increase in pressure in the cephalopedal sinus and, as the pneumostome is open, an increase in lung volume. The increase in blood pressure in the cephalopedal sinus causes a partial extrusion of the animal, whilst the increase in lung volume, on relaxation of the muscular floor, maintains the animal at its partially extruded position (during this phase the pneumostome is closed). Full extrusion is achieved after several consecutive contractions of the mantle-cavity floor (Dale, in preparation). The contracted mantle-cavity floor is returned to its normal position by the pressure of the blood in the cephalopedal sinus. As stated previously, the pneumostome is closed during this phase so that the decrease in lung volume results in an increase in lung pressure and presumably gaseous exchange is enhanced.

The buccal bulb and the oesophagus are held against the floor of the cephalopedal sinus by a non-muscular septum which is continuous with the tentacular septal sheaths. Blood pressure serves to hold the pharyngeal mass, particularly the lips, against the substratum to facilitate feeding. Schmidt (1916) suggests that a direct arterial supply of blood serves to stretch the radula membrane; however, this is by no means conclusive and requires a detailed study. A pharyngeal retractor muscle, again a branch of the columella muscle, opposes blood pressure to withdraw and practically invaginate the feeding apparatus when required.

In the head, circular, longitudinal, posterior oblique, anterior oblique, and labi levator muscles (Trappman, 1918) effect body movements and are all antagonized by blood pressure. Meisenheimer (1912) shows that protrusion of the penis of *Helix pomatia* is achieved after several convulsive contractions of the animal. It appears therefore that a higher pressure than normal is required in the cephalopedal sinus for penis eversion and this is achieved by consecutive contractions of the body-wall musculature. A retractor muscle attached to the mantle-cavity floor withdraws the penis after copulation.

Jones (1973, in preparation) and Morton (1967) suggest that blood pressure is necessary to depress waves which pass along the sole of the foot during locomotion. It has been calculated that the blood in the small haemocoelic spaces of the foot is at a pressure in the range 8–16 cm. The foot of *Helix* is very muscular and local muscular

contractions will cause variations in this pressure. This high venous pressure, together with the fact that there are no rigid skeletal elements in the foot, strongly suggest that muscular contraction must be opposed by blood pressure. A further function of blood pressure, which receives little attention, is the formation of mucus. Burton (1965*b*) shows that mucus is an ultrafiltrate of the blood, whilst Machin (1964) demonstrates that mucus production in *Helix pomatia* is dependent on the hydrostatic pressure of the blood. A saline pressure of 10 cm exerted on the inner surface of isolated pieces of *Helix* skin is sufficient for the cells to extrude enough mucus to keep the skin moist (Machin, 1964). As mucus is necessary for locomotion the estimated value of pressure in the haemocoelic spaces of the foot appears to be of the correct order.

Depending on the requirement of the animal, the ratio of visceral blood volume to cephalic blood volume can be modified. When active a large proportion of the total blood volume is required in the head and foot for the hydraulic functions mentioned above. As the visceral sinus is the only other large reservoir of blood, this increase in cephalic blood volume must be achieved by a reduction of the blood volume in this sinus. On retraction a large proportion of the blood present in the cephalopedal sinus must be accommodated elsewhere as the head is almost totally invaginated; again the visceral sinus is the only reservoir large enough to accommodate this volume of blood. Brown (1964) has shown that in *Bullia* blood passes from the cephalic sinus to the visceral sinus, during retraction, via a distinct vein. There is no such vessel in *Helix*; during retraction, blood flows directly from the cephalopedal sinus into the sub-renal and visceral sinuses and vice versa during extrusion. As there are no muscles in the viscera any change in blood pressure must be a result of a change in blood volume; a decrease in visceral sinus blood pressure occurs during extrusion (Fig. 5*b*), a result of a decrease in blood volume, whilst on retraction there is an increase in visceral sinus blood pressure (Fig. 5*a*) a consequence of an increase in blood volume. Following the initial movement of blood it is to the animal's advantage, if it is to remain in a particular state, that the modified ratio of visceral blood volume to cephalic blood volume remains constant. For instance, when the animal is extended and active the ratio visceral blood volume to cephalic blood volume is determined by the relative amounts of blood which flow down the posterior and anterior aortae. On retraction the ratio, as shown, is modified with an increase in visceral blood volume and a corresponding decrease in cephalic blood volume. If the same proportion of arterial blood continues to flow to the cephalopedal sinus the modified ratio will quickly be returned to its previous value, cephalic blood volume will increase and this will tend to extrude the animal.

In what now follows a possible mechanism responsible for the regulation of this ratio is described. When actively extending, both the amplitude and more importantly the frequency of ventricular beat increase. If we compare the ventricular trace of an active animal (Fig. 3) to that of an inactive animal (Fig. 6*d*) we see that increase in frequency is achieved by a reduction of the diastolic phase. Chadwick (1962) suggests that blood only flows down the posterior aorta during ventricular diastole because at systole the second aortic valve occludes the opening to the posterior aorta and all the blood flows down the anterior aorta. In the active, extended animal the systolic phase of the ventricle dominates the ventricular beat, ensuring an adequate supply of blood

to the head and foot. When the animal is retracted the diastolic phase is much longer than the systolic phase (Fig. 6*d*), therefore relatively more blood will flow to the viscera. This mechanism also allows visceral sinus blood to remain at a lower pressure than cephalopedal blood though both are filled from a common pressure source.

In an active, extended animal the ventricle is pumping blood into the aorta at a pressure of up to 35 cm and at a frequency up to 60 beats/min, whilst in the retracted animal ventricular systolic pressure is barely 20 cm and the frequency drops to less than 20 beats/min. Thus with an increase in activity blood pressure in the aorta increases, and furthermore, by the above-named mechanism, a correspondingly larger volume of blood flows to the cephalopedal sinus. If the body-wall musculature was responsible for the high haemocoelic pressure of pulmonates on extension there would be no need for this increase in cardiac output. The importance of the heart in maintaining the blood pressure can be easily demonstrated by severing the aorta proximal to the ventricle, whereupon the animal immediately collapses.

SUMMARY

1. Blood pressure has been measured in several parts of the haemocoel of a representative terrestrial pulmonate, *Helix pomatia*.
2. A venous pressure of 8 cm of water is required to overcome the resistance presented by the branchial plexus and to effect the process of ultrafiltration in the renal plexus.
3. Visceral sinus and sub-renal sinus blood is at a pressure barely exceeding this value and need only perform the two named functions before returning to the auricle.
4. Blood in the cephalopedal sinus and general haemocoel of the foot is at a higher pressure, of up to 16 cm, and has obvious hydraulic functions. Partly by review of the literature and partly by direct observation these functions are discussed.
5. The distribution of blood during different states of activity and the importance of the heart in maintaining the high haemocoelic pressure of pulmonates is also briefly discussed.

I thank Professor R. Dennell and Professor E. R. Trueman for research facilities and Dr H. D. Jones for valuable discussion and criticism. This work was carried out during the tenure of a Science Research Council studentship.

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