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THE FUNCTION OF THE CONUS ARTERIOSUS IN THE PORT JACKSON SHARK, *HETERODONTUS PORTUSJACKSONI*

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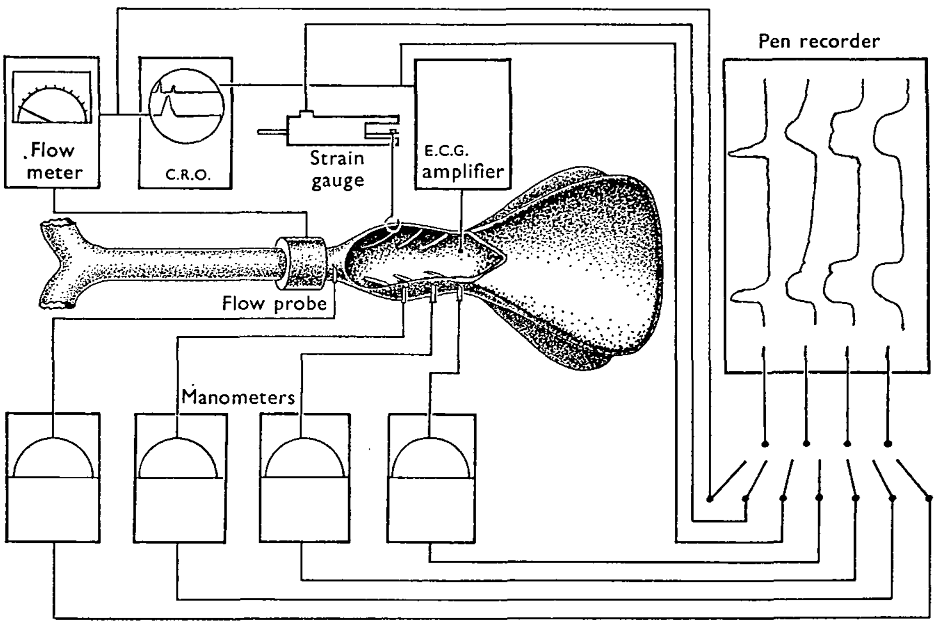
The conus arteriosus is a muscular chamber interposed between the ventricle and ventral aorta in Elasmobranchii, Holocephalii and the more primitive families of bony fish. Since Duverney (1702) suggested that it functioned as an extra ventricle, it has been variously regarded as an elastic reservoir to minimize pressure fluctuations (Keith, 1924; Daniel, 1934), an accessory pumping chamber (Gegenbaur, 1866, Stöhr, 1876, Sudak, 1965), and a valvular structure to regulate the out-flow of blood from the ventricle (Home, 1823; Pettigrew, 1864; March, Ross & Lower, 1962). Both the conal pressure recordings of Sudak (1965) in *Mustelus canis* and the cinematographic analysis of March *et al.* (1962) in *Triakis semifasciatus* show that conus systole occurs prior to ventricular relaxation. However, our knowledge of the sequence of the valve movements is still largely conjectural. This paper reports an investigation of conal function in the Port Jackson shark, *Heterodontus portusjacksoni*. The anatomy of the conus will be briefly described, and a hypothesis of its mode of action will be outlined. The evidence for this will then be presented, and the function of the conus discussed.

ANATOMY OF THE CONUS ARTERIOSUS

The conus wall consists of a thin layer of cardiac muscle overlying an elastic fibrous coat. It is equipped with three sets of valves which will be referred to as lower, middle and upper conal valves. The lower ones are near the conus-ventricular junction, and the upper ones are near the conus-ventral aorta junction. There are three semilunar valves in each set; the middle and lower valves (Pl. 1) differ from the upper ones in three respects. They are smaller and cannot bridge the lumen of the relaxed conus; they have their free edges anchored to the wall of the conus by chordae tendineae, and their free edges are subdivided into smaller lobes. Moreover, a variable number of much smaller valve cusps are interposed between the main ones of the middle and lower sets. There is some variability in the position of the middle set of valves. It is often nearer the lower set than the upper one. The middle valves divide the conus into two parts which will be termed the upper and lower conal chambers.

MATERIAL AND METHODS

Trawled Port Jackson sharks, 8–12 kg. in weight, were kept in a swimming bath and fed weekly. They were secured in circulating sea water in a constant temperature room maintained at $17 \pm 1^\circ$ C. The pericardium was opened using Tricain as a local anaesthetic. Blood pressure was recorded from the sites shown in Text-fig. 1 using strain gauge manometers (Statham P23 GC) and fine steel cannulae made from the tips of no. 22 hypodermic needles. The manometers were repeatedly calibrated by recording known pressures, using the water surface of the tank as zero level. Flow was recorded with a gated sine wave electromagnetic flow meter from a 6 mm. diameter flow probe that encircled the ventral aorta at its origin from the pericardium. Conal movement was monitored with a heart hook, wire and strain gauge. The conal electrocardiogram was recorded with a unipolar electrode. The records were displayed on a four-channel polygraph. The fish were usually curarized and maintained under artificial respiration. Heparin was injected when the surgery was complete. The results are derived from twenty-six successful experiments.

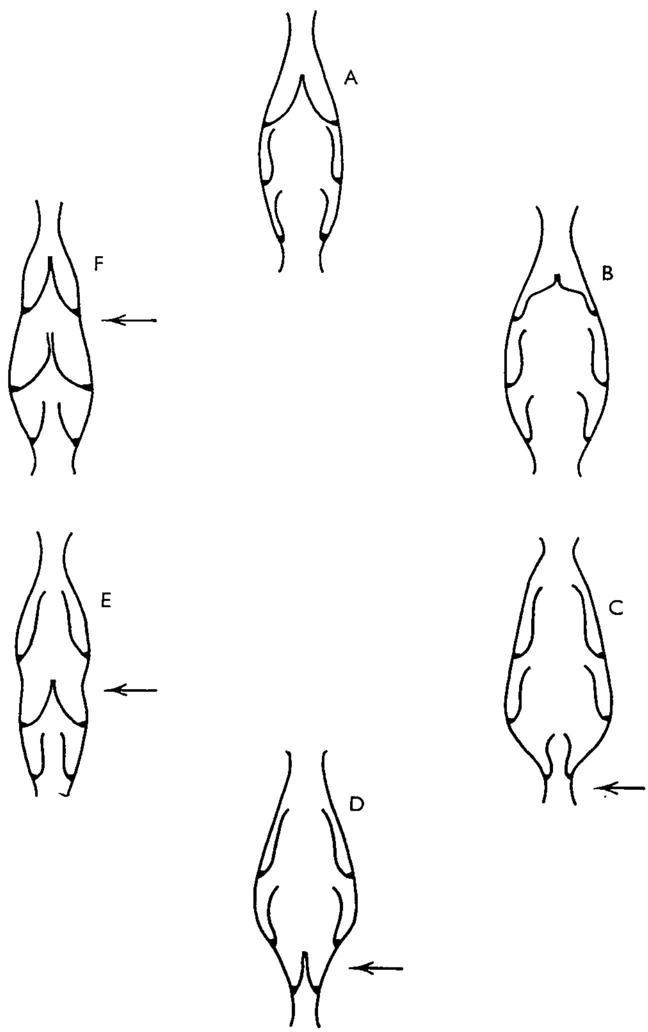


Text-fig. 1. Diagram showing sites of recording in the conus arteriosus.

Johansen (1965) has shown that the negative pressure generated within the pericardium by ventricular ejection plays a part in returning blood to the heart, and has suggested that opening the pericardium may bring about a reduction in cardiac output. Records of flow and blood pressure in the ventral aorta of *Heterodontus* made with the pericardium intact, closely resembled those made with the pericardium opened. It seems unlikely that the basic sequence of events in the conus arteriosus were changed by opening the pericardium.

THE EVENTS OF THE CONAL CYCLE: A HYPOTHESIS

During the later part of diastole (Text-fig. 2A), the conus is in communication with the ventricle, and the upper semilunar valves are closed. With the onset of ventricular systole, blood is forced into the conus which passively dilates and the upper valves bulge (Text-fig. 2B). As the pressure rises towards, and exceeds, that in the ventral aorta, the upper valves are pushed open. The blood in the ventral aorta is accelerated rapidly forwards. Halfway through ventricular systole, the conus starts to contract bringing the lower set of semilunar valves closer together (Text-fig. 2C). The wave of contraction spreads rostrally, squeezing the moving stream of blood just before

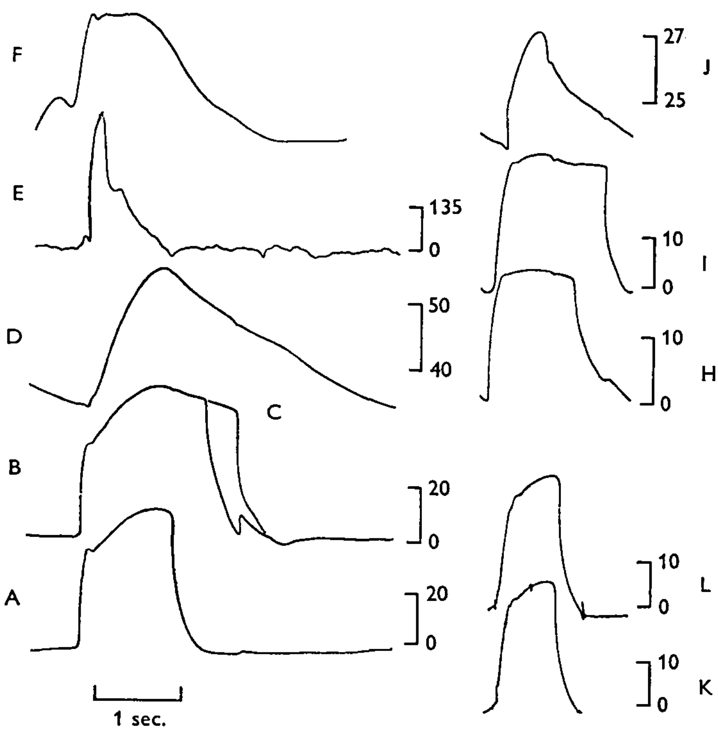


Text-fig. 2. Diagram of the events of a conal cycle. A = towards the end of ventricular diastole. B = onset of ventricular systole. C–F = conal systole. The arrow indicates the zone of contraction.

ventricular systole comes to an end. The blood in the lower part of the conus is forced backwards, closing the lower valves which are now close enough together (Text-fig. 2D) to be competent. As the wave of conal contraction spreads forwards, the middle valves are closed in like manner, and the lower ones open (Text-fig. 2E). Blood flow in the ventral aorta ceases as the lower valves close. There is normally little or no backward flow at this time. The wave of conal contraction passes forwards (Text-fig. 2F) bringing the bases of the upper valves closer together. This coincides with the relaxation of the lower conus; as the middle valves are not large enough to bridge the cavity of the relaxed conus, they fall apart and a brief back flow from the ventral aorta closes the upper valves. These have large cusps and remain closed as the conus relaxes.

THE EVIDENCE FROM PRESSURE AND FLOW RECORDINGS

The instant at which each of the three sets of valves opens and closes can be identified on the principle that, prior to closure, pressures recorded above and below a valve will follow each other and that no chamber can sustain a pressure greater than



Text-fig. 3. Pressures in, A, K, L, the ventricle. B, H, the lower conal chamber. C, I, the upper conal chamber. D, J, rostral to the upper conal valve. Calibrations in cm. H_2O. E. Blood flow in ventral aorta, calibrations = ml./min. F. Movement of the conal wall; downward pen deflexion = contraction. The tracings A, B, C, D, E, F, are all from one fish, with A, B, D, E, recorded simultaneously. H, I, J, are simultaneous recordings from another fish. K and L are successive recordings from a third fish. Traces B and C have been superimposed.

the one caudal to it unless the valve between is closed. On this criterion, it is clear from Text-fig. 3A, B and C, that during the latter part of diastole, and throughout auricular systole, only the upper valves were closed, the conus being in free communication with the ventricle. With the onset of ventricular systole, pressure in the ventricle, and in the posterior and anterior conal chambers, rose rapidly. The conus in the living animal can be seen to expand at this time; the small elevation in the ventral aortic pressure trace (Text-fig. 3D) and in the flow record (Text-fig. 3E) are presumably due to the upper conal valves bulging under the impact of the entering blood. March *et al.* (1962), in their cinematographic analysis of the conus of *Triakis*, noted dilation of the conus with the onset of ventricular systole.

As conal pressure rose to, and exceeded, that in the ventral aorta (Text-fig. 3 D), the upper valves opened and ventral aortic pressure followed that of the ventricle and conus. Simultaneously the blood flow in the ventral aorta (Text-fig. 3 E) accelerated to a maximum and then decelerated.

The closure of the lower conal valve can be inferred when the ventricular pressure fell towards zero whilst that in the conus was maintained. That this closure was effected by conal systole is shown by the lower conal and ventricular pressure records. The closure of the lower conal valves caused a characteristic oscillation on the trace; it occurred before the onset of ventricular relaxation and the fall of ventricular pressure (Text-fig. 3 A, B). Sudak (1965) has reported this in *Mustelus canis*. The strain gauge records of the movement of the conal wall (Text-fig. 3 F) supported this. The downward movement of the pen (Text-fig. 3 F) indicated decreasing diameter of the conus. Halfway through ventricular systole, when ventricular pressure was still rising, the base of the conus started to narrow. This early contraction could be recorded only at the base of the conus. Records taken more rostrally showed conal systole occurring progressively later. March *et al.* (1962) concluded that the conus of *Triakis* contracted late in ventricular systole. The flow record (Text-fig. 3 E) showed little or no back flow associated with closure of the lower conal valve. The flow probe was placed just rostral to the conus, so this was to be expected if the back flow that closed the lower conal valve was generated posterior to it.

The evidence of the separate closure of the middle conal valve is seen in the separation of the pressure records made in the upper and lower conal chambers (Text-fig. 3 B, C, H and I). In some experiments, the record of pressure in the upper conal chamber showed a valvular oscillation as the middle valve closed, and again it occurred just prior to the fall of pressure in the lower conal chamber (Text-fig. 3 H, I). This again suggests that the middle valve was closed by back flow generated by the contraction of the upper conal chamber. Commonly this event was not recorded on the flow trace, though there was sometimes a slight indication of back flow from the ventral aorta.

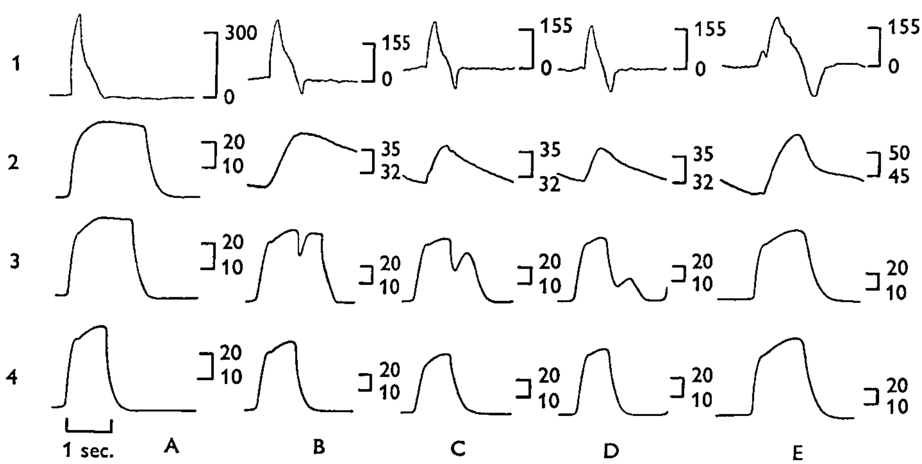
The opening of the middle conal valve could be inferred when the pressure in the upper conal chamber fell towards zero (Text-fig. 3 C, D, I and J). This was accompanied by a second valvular oscillation on the ventral aortic pressure trace (Text-fig. 3 J), which maintained a steady decline in pressure towards the diastolic level. The upper valve must have closed as the middle valve opened; a slight back flow was sometimes recorded coincident with this (Text-fig. 6, 1 A, B) and may be ascribed to the opening of the middle valves and the closure of the upper ones. Unlike the closure of the lower and middle valves, that of the upper one was synchronous with the decline in pressure below it. This was to be expected if this valve was closed by back flow from the ventral aorta.

The flow traces (Text-figs. 3 E; 6, 1 A, B) bring out clearly that the flow of blood into the ventral aorta was virtually confined to the period between the opening of the upper conal valves and the closing of the lower ones. Flow was at or near zero throughout the remainder of the cycle.

Two other events of the cardiac cycle were sometimes recorded in the ventricular pressure traces and are noted here. The closing and opening of the atrioventricular valves sometimes initiated visible oscillations (Text-fig. 3 L). A valvular oscillation halfway through ventricular systole may possibly have been due to one of the lower conal valves vibrating in the stream of ejected blood as conal systole commenced (Text-fig. 3 K).

THE EVIDENCE DERIVED FROM ANAESTHETIZING THE CONUS

The conus muscle was anaesthetized by placing crystals of tricain on its surface. The first recordable impairment of conal function was seen almost at once: it was a delay in the start of conal systole so that the ventricular pressure had begun to fall before the lower conal valves closed (Text-fig. 4 B 3). This resulted, as would be expected from the hypothesis outlined earlier, in back flow from the ventral aorta (Text-fig. 4 B 1). With further weakening of the conal musculature the lower and middle valves became incompetent, and the resulting back flow closed the upper conal valves.



Text-fig. 4. Simultaneous records of flow in the ventral aorta (channel 1) and of pressure in the ventral aorta (2), lower conal chamber (3) and ventricle (4), during the progressive anaesthetization of the conus. Record A (before anaesthetization). In A, channel 2, recorded pressure in the upper conal chamber. In B–E, this was switched to record ventral aortic pressure. Between D and E, 8 μg./kg. of adrenalin was injected. Calibrations in cm. H_2O and ml./min.

This can be inferred from Text-figs. 4, 3 C and D, where the conal pressure (+30, +10 cm. H_2O) was less than that prevailing in the ventral aorta of that time (+34, cm. H_2O). The pressure recorded in the conus was that developed by the enfeebled muscle forcing blood past the incompetent lower valve. The role of the lower conal valve in separating the ventral aorta from the ventricle was assumed by the upper conal valve as the conal muscle weakened.

In Text-fig. 4 E, the blood pressure was elevated by adrenalin (8 μg./kg.) and the full extent of conal paralysis could then be seen. The conal pressure trace (Text-fig. 4 E 3) resembled that of the ventricle (Text-fig. 4 E 4). The back flow had increased from 6·8 ± 2·2 % in Text-fig. 4 A 1, to 30·8 ± 5·4 % in Text-fig. 4 E 1. This back flow caused the ventricle and conus to dilate. The contour of the ventral aortic pressure (Text-fig. 4 E 2) shows the rapid early fall characteristic of valvular incompetence.

Under these circumstances the only valves large enough to span the conus would have been the upper ones. All these changes were seen in reverse order as the conus recovered from the anaesthetic.

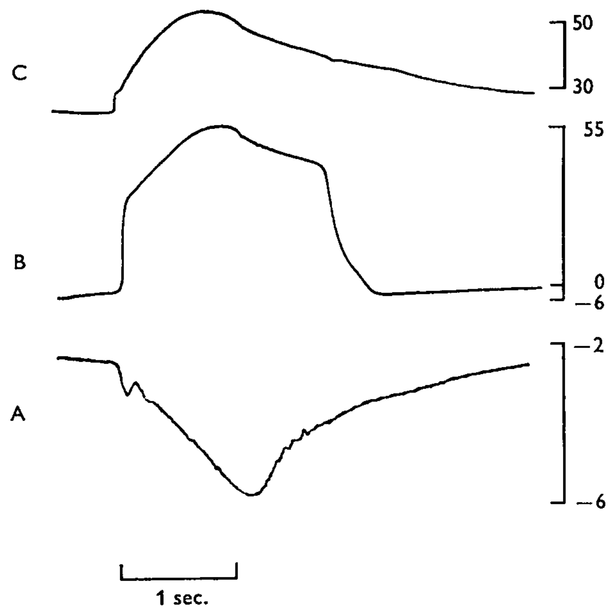
THE EVIDENCE FROM THE EXCISED HEART

In a dead isolated heart it was easy to demonstrate that fluid injected into the ventral aorta did not pass into the ventricle and that the upper conal valves were perfectly competent even in a dead preparation. If they were held open by a small segment of glass tube passed up from the ventricle, it was not possible to make the lower conal valves competent. They were not large enough to bridge the conus and must therefore, in life, depend on the contraction of the muscle ring around their bases to reduce the lumen of the conus to a diameter they can bridge.

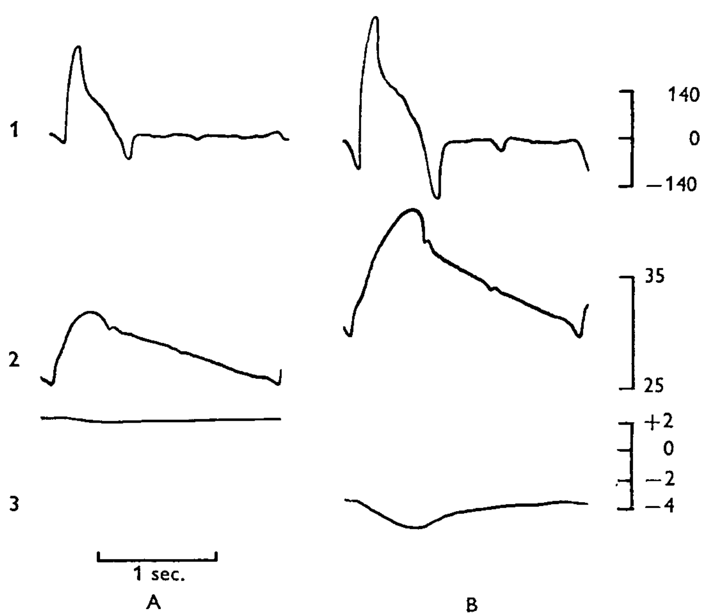
DISCUSSION

The pressure records from the ventral aorta of *Heterodontus portusjacksoni*, *Squalus acanthias* (Satchell, 1960) and *Mustelus canis* (Sudak, 1965), are alike in showing two valvular oscillations signalling the closing of the lower and upper conal valves. During the period between the opening of the upper conal valves and the closing of the lower ones, the ventricle ejects its blood into the ventral aorta, and both the flow of blood through, and the rise of pressure in, this vessel may correctly be ascribed to ventricular systole. The period following this, and lying between the closure of the lower and upper conal valves, corresponds to conal systole. In the past it has been customary to assume that the pressure was maintained during this period by the active contraction of the conus and that it served to sustain blood flow through the aorta and branchial vessels during at least part of ventricular diastole (Satchell, 1960; March *et al.* 1962; Johansen & Martin, 1965; Sudak, 1965). The flow-meter record does not support this, and the pressure records can be interpreted differently. During this period, when conus and ventral aorta are in communication and share a common pressure profile, the pressure declines steadily towards the diastolic level. The record does not differ significantly from that of a mammal, which has no conus; both may be interpreted as a distended elastic reservoir passively emptying through the resistance of the peripheral vessels. Such pressure as there is in this period is primarily due to the distension of the elastic reservoir by the previous ventricular ejection. There is no obvious secondary pressure rise that can be attributed to conal systole. In fact, the flow-meter records show that during conal systole flow is at or near to zero. There is thus no reason to regard the conus as an extra pumping chamber that prolongs the period of flow through the gills.

An alternative view of conal function is that it is primarily concerned with postponing the instant when the upper conal valves must be closed by back flow to a time when the negative pressure in the pericardium, generated by ventricular ejection, has declined to its minimum value. Johansen (1965) has shown that such pressures are developed in *Squalus suckleyi* and has suggested that they play a part in returning the blood to the heart. The problem of venous return in the Port Jackson shark is currently under investigation by Mr R. Holst, and he has kindly lent me the tracings from one of his experiments (Text-fig. 5 A–C). At the conclusion of ventricular ejection a



Text-fig. 5. Simultaneous records of pressure in, A, the pericardium; B, the anterior conus; C, the ventral aorta. Calibrations in cm. H_2O. Trace supplied by R. Holst.



Text-fig. 6. The effect of pericardial pressure on backflow in the conus. Channel (1) flow in the ventral aorta; channel (2) pressure in the ventral aorta; channel (3) pressure in the pericardium. Between A and B the pericardial pressure has been made more negative. Calibrations = cm. H_2O and ml./in.

negative pressure approaching -6 cm. H_2O was developed. Pressures as low as -12 cm. H_2O have been recorded in anaesthetized fish of this species. The conus lies within the pericardium and is subject to these negative pressures, which must act to pull the upper conal valve bases apart. A negative pressure outside the conus is presumably more likely to make the valves incompetent than an equivalent positive pressure in the ventral aorta, where a component of the pressure serves to press the upper conal valves together. This hypothesis has been tested by recording flow in the ventral aorta whilst the intact pericardium was subjected to positive or negative pressures from a pressure reservoir. Changing the intrapericardial pressure from $+2$ cm. H_2O (Text-fig. 6A) to $-4 \cdot 5$ cm. H_2O (Text-fig. 6B), when the average ventral aortic blood pressure was 28 cm. H_2O increased the back flow from $12 \cdot 1 \pm 2 \cdot 6$ % to $19 \cdot 2 \pm 4 \cdot 7$ %. When the average ventral aortic pressure was raised to 39 cm. H_2O by injecting 2 mg./kg. of adrenalin, a change of intrapericardial pressure from $+2$ cm. H_2O to $-2 \cdot 4$ cm. H_2O increased back flow from $11 \cdot 4 \pm 2 \cdot 4$ % to $29 \cdot 1 \pm 7 \cdot 7$ %. The increased ventral aortic pressure did not, on its own, increase back flow. A notable feature (Text-fig. 61B) was the presence of a period of back flow as the upper conal valves opened. This suggests that the negative intrapericardial pressure combined with the dilation of the conus by ventricular ejection to pull the upper conal valves apart an instant before the conal pressure had risen to the level of that in the aorta.

It may be surmised that the reduction of back flow is important because of the harmful effect it would have on the efficiency of the counter-current arrangement of water and blood flow in the respiratory lamellae. If appreciable back flow occurred, oxygenated blood would be shunted back into regions where the oxygen tension of the water was low and the diffusion gradient would be reduced or reversed. The hypothesis of conal function advanced in this paper thus links the presence of a muscular valved conus with the existence of a semi-rigid pericardium and a negative intrapericardial pressure. Only further research will show whether this is a valid generalization.

SUMMARY

1. Blood pressure recordings were made above and below each of the three tiers of valves in the conus of *Heterodontus portusjacksoni*. Flow in the ventral aorta was recorded with an electromagnetic flow-meter.

2. It was shown that the lower conal valves close first and that this closure occurred before the end of ventricular systole.

3. The middle conal valves closed before the lower ones opened. The closure of both of these sets of valves was caused in part by the circumferential decrease due to conus systole, and in part by the back flow this engendered.

4. The upper conal valves closed as the middle ones opened at the end of conal systole.

5. Paralysing the conus with topical tricain rendered the lower and middle conal valves incompetent and caused the upper conal valves to be closed following ventricular relaxation with an increase in back flow.

6. The hypothesis is advanced that the conus serves to postpone the closure of the upper tier of valves until the negative intrapericardial pressure generated by ventricular ejection has decayed to a lower value.

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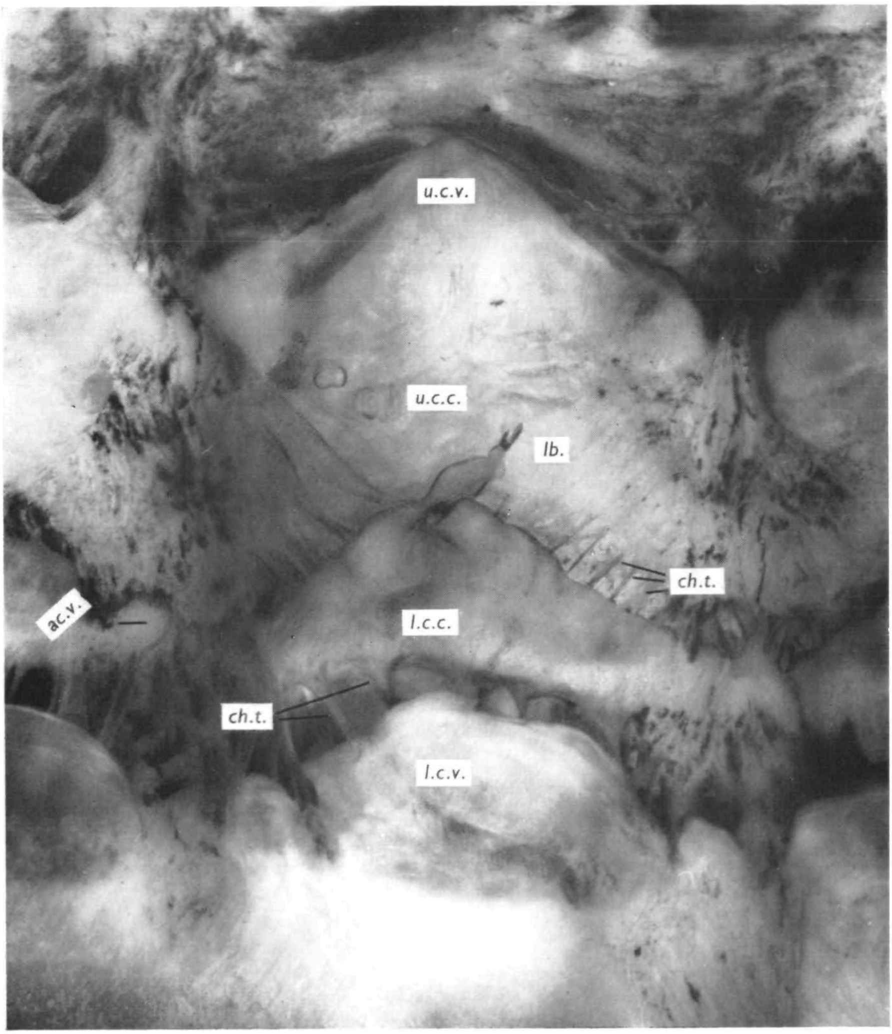
EXPLANATION OF PLATE

The ventral series of valves in the conus of *Heterodontus portusjacksoni*. *ac.v.* accessory valve cusp, *ch.t.* chordae tendineae, *l.b.* lobe of middle conal valve, *l.c.v.* lower conal valve, *l.c.c.* lower conal chamber, *u.c.c.* upper conal chamber, *u.c.v.* upper conal valve.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