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Circulatory physiology of *Nautilus*

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Summary. Present information places the circulatory performance of *Nautilus* at the bottom of the cephalopod scale but shows it to be distinctly different from that of gastropods and bivalves. The feature which clearly places it closer to its coleoid relatives than to other groups of molluscs is the enhancement of the branchial circulation by the beating pericardial glands and renal appendages. These organs have their homologues in the coleoid pericardial chamber. Recently, studies of living embryos show that the development of a functional circulatory system is an early event during ontogeny and that this information may have important implications for our understanding of the evolution of a branchial circulation.

Key words. Cephalopod; *Nautilus*; heart function; arterial function; windkessel; capacitance vessels; microcirculation.

Introduction

Ever since Owen[21] published descriptions of the soft parts of *Nautilus,* zoologists and paleontologists have hoped that studies of living *Nautilus* would shed light on possible modes of existence of the once-dominant nautiloids and ammonites, as well as aid in understanding cephalopod evolution. In the ensuing discussion an attempt is made to examine the functional attributes of the *Nautilus* circulatory system and to place these features in the context of circulatory-system function in the coleoids and in other molluscs.

Anatomical framework of the Nautilus circulation

The definitive anatomical study of *Nautilus pompilius* was produced by Griffin[14] in 1900. He included an extensive description of the gross circulatory anatomy. Figure 1 shows the major elements in the *Nautilus* circulation.

A useful device for discussing the functional properties of the *Nautilus* circulatory system is the scheme devised for *Octopus* circulation by Johansen and Martin[16]. These workers proposed that seven functional elements exist as follows: 1) Two types of active circulatory pumps; the systematic heart and the branchial hearts. 2) A passive pump; the respiratory apparatus conveying pressure changes to the large, thin-walled elements of the vascular system. 3) The propulsive vessels; vessels which actively propel blood, e.g., the branchial vessels. 4) The 'windkessel' vessels; the aortae and their major branches. 5) The resistance vessels; the terminal portions of the arterial system. 6) The exchange vessels; the capillaries and sinuses. 7) The capacitance vessels; the distensible, thin-walled vessels such as the vena cava.

Heart function

The major propulsive organ in the circulation of *Nautilus* is the systemic ventricle which produces a systolic pressure that averages 3.43 kPa (range 0.78–7.85 kPa) in the dorsal aorta[9]. By using stress-extension curves, Gosline and Shadwick[13] determined that the normal physiological range in the dorsal aorta was from 1.96 to 5.89 kPa. A comparison of *Nautilus* ventricular performance to that of other molluscs clearly demonstrated that *Nautilus* is at the bottom of the range reported for cephalopods but exceeds that of molluscs from other classes.

Based on ultrastructural evidence, Dykens et al.[10] suggested that the *Nautilus* ventricular myocardium is not as well developed as that of squid. However, a study of the enzyme profiles of the *Nautilus* ventricle[15] indicated that metabolism is primarily aerobic, thus implying that the ventricle beats continuously to deliver oxygen and other nutrients to the rest of the body. There are no examples of the *Nautilus* ventricle stopping spontaneously like that of several gastropods[5], a phenomenon indicative of a higher anaerobic capacity of the heart; a capacity that was found in the heart of the gastropod, *Busycon*[11].

In *Octopus* and other coleoids, the other active pump is that which drives the blood through the branchial part of the circulation. Although Willey[29] first described the pulsations of the renal and the pericardial glands at the base of the afferent branchial vessels in *Nautilus,* and Naef[20] referred to their heart-like function, the standard position of textbooks and other secondary sources is to view the active branchial circulation as a coleoid and not a nautiloid feature.

Bourne et al.[8,9] demonstrated that there is a significant increase in the pressure of the blood as it passes from the vena cava to the afferent branchial vessels (fig. 2). In afferent branchial vessels, blood pressure averaged 0.42 kPa while that of both the vena cava and efferent branchial vessels had mean values close to 0 kPa, occasionally dropping below ambient. This information confirmed that there was pressure assistance through the branchial circulation, thus indicating that special branchial pumps are a cephalopod characteristic. The arrangement for pumping branchial blood and for excretion is somewhat different in nautiloids from that in coleoids, but clear homologies exist for these structures[19,24].

Arterial function

'Windkessel' vessels were first proposed by Otto Frank[12] to account for the ability of mammalian aortae and their higher resistance terminals to act as the hydraulic analogue of resistance-capacitance filters in electricity and to convert the pulsatile pressure output of the ventricle into the smoother pressure profile seen in the more distal parts of the circulatory system. Johansen and Martin[16] applied this model to *Octopus dofleini* circulation and this applicability was later supported by Shadwick and Gosline[25]. The works of Bourne et al.[9] and Gosline and Shadwick[13]

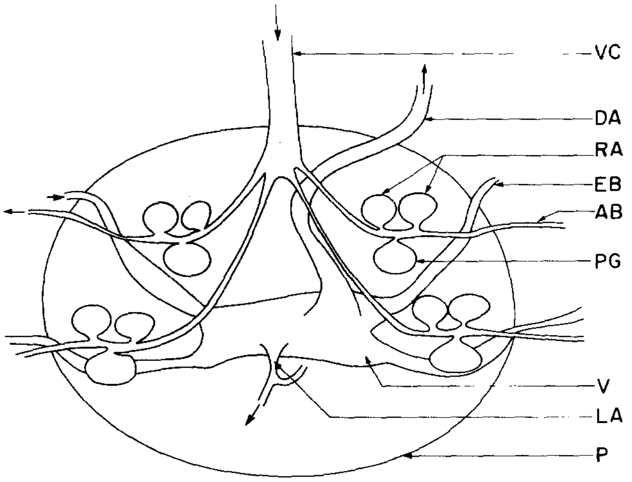

Figure 1. A ventral view of the major elements of the circulatory system associated with the pericardial chamber of *Nautilus*. AB, afferent branchial vein; DA, dorsal aorta; EB, efferent branchial vein; LA, lesser aorta; P, pericardium; PG, pericardial gland; RA, renal appendages; V, ventricle; VC, vena cava. (from Bourne et al.[9])

extend the application of the 'windkessel' model to discussion of the hemodynamics of the *Nautilus* circulation.

Nature and function of the microcirculation

Once blood leaves the arterial system it enters the exchange vessels, which in *Nautilus* appear to consist mostly of small diameter lacunae sinuses. It should be noted that an examination of several published electron micrographs did not reveal capillaries of the nature seen in squid[2,15,18,24]. Although there are no direct studies as to whether *Nautilus* can regulate flow distribution in the systemic circuit, Redmond and Bourne[23] explored vascular control in the excised branchial circulation of *Nautilus*. These workers found that a linear relationship exists between pressure and flow in the branchial circuit and that this vascular bed behaves in a 'non-reactive' or 'passive' manner. This suggests that any control exerted over flow through this region is centrally mediated and is not caused to any great extent by intrinsic factors. Furthermore, Redmond and Bourne[23] tried several putative molluscan neurotransmitters (acetylcholine, dopamine, 5-hydroxytryptamine and noradrenaline) to alter the response of the excised branchial circulation. Of the four neurotransmitters only 5-hydroxytryptamine appeared to have a possible physiological role. 5-Hydroxytryptamine at a concentration of 10^{-9} M caused vasodilation of the branchial circulation. Generally the major role assigned to 5-hydroxytryptamine in the molluscan circulation is one of cardioacceleration. It appears that the same factors that call for increased cardiac output require increased augmentation of blood flow through the gills; hence cardiac output is coupled to the state of branchial vasodilation.

Redmond and Bourne[23] discovered that dopamine mimicked the effects of 5-hydroxytryptamine on the *Nautilus* gill but that this substance had a lower efficacy and higher threshold than did 5-hydroxytryptamine. They also found that the same kinds of responses occurred in the *Octopus* gill. The lack of responsiveness of the *Nautilus* gill to acetylcholine is in contrast to vasodilation seen in squid postsystemic circulation[6].

Nautilus possesses an extensive capacity to alter aortic diastolic pressure while at the same time keeping the return pressure to the heart constant[9]. The phenomenon indicates a change in the cardiac output-total peripheral resistance interaction, suggesting some capacity to alter the systematic vascular bed.

The nature of the capacitance vessels

In *Nautilus* the capacitance vessels, represented by the dorsal hemocoel, other sinuses, the vena cava and the efferent branchial vessels, appear as an important factor in maintaining effective circulation by forming a variable volume reservoir[9]. The ventilatory pump acting on the capacitance vessels was found to play a profound role in maintaining effective circulation[9]. In *Nautilus* the ventilatory movements and waterjet for locomotion are produced by undulating contractions of the funnel base[3,28]. More vigorous ventilation and rapid locomotion are brought about by protraction and retraction of the head utilizing the head muscles[22,26]. This ventilatory action rhythmically interacts with the capacitance vessels to couple venous return physically to respiratory activity and locomotion.

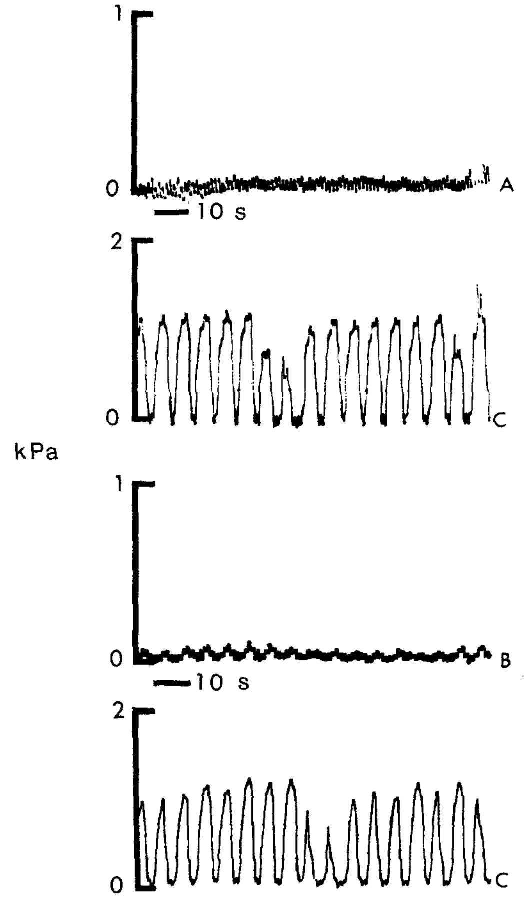

Figure 2. Blood pressure recorded from afferent and efferent branchial vessels and vena cava of *Nautilus* showing the increased pressure in the afferent branchial vessel (C) compared with the lower pressure entering this area from the vena cava (A) and leaving the gills in the efferent branchial vessel (B). (From Bourne et al.[8])

This action is analogous to the 'venous pump' that aids in the return of blood to the heart during activity as described in any textbook of mammalian physiology. Although operationally different, this interaction of ventilation and circulation is similar to that seen in coleoids[4,16,27].

Flow and cardiac output

Since the performance of a circulatory system is measured by its ability to deliver oxygen and metabolites to tissues, an evaluation of cardiac output is an indication of this ability. Cardiac output is the blood pumped from the heart in unit time. Johansen et al.[17], using the Fick method, calculated a cardiac output of $51.6\ \mathrm{ml\,kg^{-1}\,min^{-1}}$ for *Nautilus* at 17 °C, a value which is at the lower end of the cephalopod scale.

Using electromagnetic flowmetry, Bourne et al.[9] discovered that there was a brief, sharp flow reversal in the flow pulse of the dorsal aorta. The contour of this pulse was thus more mammal-like than it was aracheogastropod-like[7]. In the latter the action of an aortic bulb prevents the sharp flow reversal[7].

In short, one is struck more by the similarity to than by the differences from coleoid cardiovascular function. Whatever differences may exist can be accounted for by the added requirement of the coleoid system to operate at the higher levels necessary to sustain the more active lifestyle of the latter group.

Ontogeny of circulatory function

Recently, and for the first time, Arnold and Carlson[1] observed living *Nautilus* embryos. Of particular interest here is the early appearance of a circulation whose function is to transport materials between the massive yolk and the embryo proper. These are the first descriptions of an invertebrate with an extra-embryonic circulation. Furthermore, Arnold and Carlson[1] indicated that this early circulation is driven by the rhythmic contractions of the yolk sac and the lateral areas between the mantle and funnel primordia. They suggested that in coleoids the latter regions would represent the areas where the branchial hearts and vena cava develop. This information has important ramifications in our understanding of the evolution of a branchial circulation in cephalopods, for it may suggest that what now appears as branchial pumps was developed as the functional, early embryonic hearts for delivering nutrient to the embryo from the yolk.

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