CONTROL OF CARDIOVASCULAR FUNCTION AND ITS EVOLUTION IN CRUSTACEA

BRIAN R. McMAHON

Biological Sciences, The University of Calgary, Calgary, Alberta, Canada T2N 1N4

e-mail: mcmahon@acs.ucalgary.ca

Summary

Work in the last decade has shown that crustacean open circulatory systems are highly efficient and controlled in a complex manner. Control occurs at several levels. Myocardial contraction is initiated in the cardiac ganglion but constantly modulated by the central nervous system, both directly via the cardioregulatory nerves and indirectly via the neurohormonal system. Heart rate and stroke volume can be controlled independently and measurements of both are needed to assess cardiac output accurately. Haemolymph outflow from many arthropod hearts is via a complex multiarterial distribution system, and the regional distribution of cardiac output is tightly controlled via cardioarterial valves at the base of each artery. These valves contain innervated muscle, and differential contraction serves to regulate the efflux of oxygenated haemolymph into a particular system. The major influence on both the evolution and control of arthropod open blood vascular systems is efficiency of oxygen uptake and delivery. This influence is illustrated by reference to a variety of crustacean and other arthropod types.

Key words: physiology, cardiovascular systems, Crustacea, Arthropoda, evolution, oxygen.

Introduction

Crustaceans, indeed arthropods generally, have an open circulatory system that can be loosely defined as a blood vascular system in which the circulating fluid (hæmolymph) passes, at some point, through tissues directly, i.e. in passages unbounded by endothelial walls. Within this definition, however, we find a very wide range of circulatory patterns ranging from exceedingly simple, i.e. no vessels present, as in some copepods or in the naupliar larval stages of the Decapoda (McMahon et al., 1995) to the extremely complex distribution systems seen in adult decapod crustaceans (Fig. 1).

This review considers the unifying factors that control the flow of hæmolymph through blood vascular systems and the roles that these factors have played in the evolution of crustacean blood vascular systems. The review will focus on the control of blood flow through the vascular system generally, rather than control of the heart *per se*, which has been more extensively studied (Cooke, 1988) and would require a separate review. Control of haemolymph flow patterns is best known from decapod crustaceans, but this paper will include details from other arthropod groups to provide an evolutionary perspective.

Ancestral vascular systems

Simple systems

From this perspective, the review should start with consideration of the most ancient systems. Within the Arthropoda, unfortunately, there is no certainty as to what form these took. Thus it is preferable to start with the simplest existing vascular systems, realizing that these may be highly modified from the ancestral form. The simplest vascular systems are organized around a single dorsal longitudinal vessel possessing segmentally arranged ostial valves and alary ligaments dividing the heart into a series of interconnected segmental chambers lying within a collecting chamber, the pericardial sinus. Blood vascular systems of this kind are found in the present-day representatives of the Remipedia and Cephalocarida, which are generally considered to be the most ancient living crustaceans. Essentially similar systems are found in many other arthropod groups, e.g. millipedes and insects as well as the Onycophora, which appear to be intermediate between annelids and arthropods, and are therefore commonly regarded as illustrating an ancient level of organization.

This level of blood vascular system organization is well illustrated by that of the brine shrimp *Artemia franciscana* (Fig. 2). Despite their apparently simple morphology, recent work in my laboratory has shown the haemolymph circulation in these animals to be relatively complex, with hæmolymph flow following highly organized, specific circuits, both within each segment and within the body generally (Fig. 2). The tubular *Artemia franciscana* heart obtains oxygenated hæmolymph from the pericardial cavity via ostial valves occurring in each segment along its length. All hæmolymph

Fig. 1. A vascular cast showing the arterial distribution system of the crab *Cancer magister*. Cast made by injection of Batson's casting resin. Photograph courtesy of C. Reiber and I. McGaw. Scale bar, 1 cm.

exits the heart anteriorly and flows over the cephalic nervous system and eye-stalks before passing back via identified channels through the tissues, eventually entering the gills present on the majority of appendages (Fig. 2). From here the reoxygenated hæmolymph passes back, again through discrete channels, to the pericardial cavity and hence into the heart. It is important to note that, even in this simplest system, we find no evidence to support the original description of crustacean circulatory systems that suggested sluggish and random movement of hæmolymph through the tissues (Maynard, 1960). Instead, the haemolymph circulation here, as in higher crustaceans, follows a few simple tenets or rules. These are as
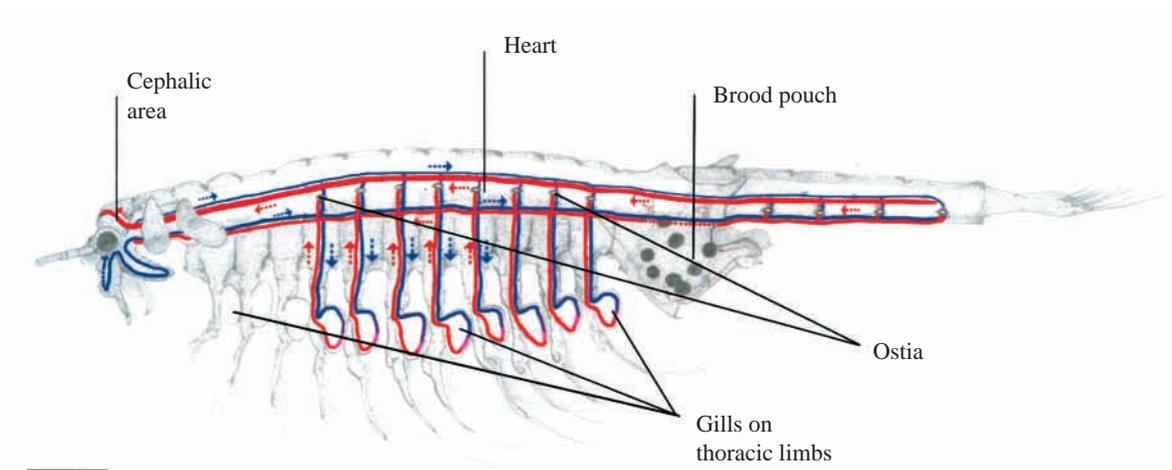

Fig. 2. Drawing of the blood-vascular system of *Artemia franciscana* to show haemolymph distribution paths. Arrows indicate the direction of haemolymph flow in the heart and within each segment. Red, oxygenated; blue, deoxygenated haemolymph. Drawing courtesy of S. Hanson. Scale bar, 1 mm.

follows: (i) a primary function of the blood vascular system is the delivery of oxygenated hæmolymph to the central nervous system and anterior sense organs; (ii) oxygenated hæmolymph follows specific, predictable, distribution pathways through the tissues and to the gills; (iii) there is little or no admixture of oxygenated with deoxygenated hæmolymph in passage from the gills to the heart.

A corollary of (iii) is that in an open system, an essential function of the pericardial sinus is to serve as a collection reservoir to isolate oxygenated haemolymph entering the heart.

Studies of small, highly modified, crustaceans such as the cladoceran *Dapnia magna,* illustrate a somewhat different but equally complex system. In *Daphnia magna* shortening of the

body has been associated with further reduction of the blood vascular system to include only a globular heart. Pirow et al. describe haemolymph flow from heart initially to the head region to perfuse cephalic structures (Pirow et al., 1999). From the head area hæmolymph flow is divided into two streams. The first flows through medial ventral lacunae to limbs 1–4, then returns via the carapace lacunae to the pericardium. Oxygenation can occur either in the branchial area or in the carapace. The second stream passes into the intestinal lacuna where it is joined by hæmolymph from limb 5. This stream perfuses the tissues before passing back to the pericardium via a separate dorsal lacuna. This degree of reduction therefore appears associated with some of admixture of oxygenated and

Fig. 3. A vascular cast demonstrating the complexity of the arterial distribution system of *Limulus polyphemus.* Cast made by injection of Batson's casting resin. Photograph courtesy of G. B. Bourne. Scale bar, 1 cm.

venous haemolymph entering the heart. Nonetheless haemolymph in the cephalic area of *Daphnia magna* is 80–100 % O_2-saturated, confirming the efficiency of the system. These morphologically simple blood vascular systems therefore are of high functional efficiency and have all the functional features of the most complex systems, differing only in the complexity of the arterial distribution system.

Complex systems

Other ancestral arthropods, however, do not have simple blood vascular systems. An excellent example is provided by the horseshoe crabs, certainly one of the most ancient living arthropod groups. In *Limulus polyphemus* a long tubular heart extends over much of the body with ostia and alary ligaments organized into a segmental series. The distribution system of this heart is, however, extremely complex (Fig. 3; Redmond et al., 1982) and because of this the heart is, of necessity, a complex muscular organ capable of developing relatively high pressures, similar to those of decapod crustaceans (Redmond et al., 1982; McMahon et al., 1997). The heart of *Limulus polyphemus* pumps hæmolymph anteriorly into three series of arterial distribution vessels, which are organized as vascular rings (Fig. 4). It is important to note that hæmolymph can leave the heart only through vessels in the prosoma. Three vessels exit from the anterior end of the heart (Fig. 4). Of these, a single vessel travels anteriorly to connect with an anterior marginal ring vessel circumnavigating the prosomal carapace. A series of short arteries leave the heart anteriorly but, once outside the pericardium, fuse to form a second ring vessel supplying the pro- and opisthosomal viscera. A pair of large vessels descend ventrally from the anterior of the heart, fusing to form a third arterial ring system, which divides to send vessels to each pair of appendages including the limbs. A remarkable feature of this ventral arterial system is that it completely surrounds the central nervous system, even including the nerves to the limbs.

This apparently unique feature may be easily explained in terms of the first basic tenet of the system, i.e. the need for adequate oxygen delivery to the central nervous tissues. In *Limulus polyphemus* this is achieved by superfusion of the entire central nervous system with oxygenated hæmolymph much in the same way as reported for *Artemia franciscana*, but with a unique development in that the superfusion occurs via an arterial distribution vessel that completely surrounds the whole central nervous system. It is noteworthy that in many crustaceans, such as isopods, stomatopods and euphausids as well as in other arthropods (and indeed in annelids and other invertebrates), the arterial blood vascular system is often closely applied to the central nervous system though not surrounding it. In the giant isopod *Bathynomus doerderleini* several ventral ganglia are surrounded by haemolymph sinuses (K. Tanaka, personal communication).

From the finest branches of the arterial distribution system within the limb muscles and other tissues, 'deoxygenated' hæmolymph is collected through an equally complex system of organized sinuses, via which it collects in a pair of ventral

sinuses (sometimes termed cardinal veins) that deliver the hæmolymph to the book gills alone. After oxygenation, hæmolymph passes from the book gills via specific branchiocardiac canals, which open directly into the pericardium only in the opisthosoma. To ensure no admixture, oxygenated hæmolymph thus enters the pericardium only in the opisthosoma and leaves the heart only in the prosoma. The ancient *Limulus polyphemus* thus has a much more complicated arterial distribution system and more muscular heart than *Artemia franciscana*, but the three basic tenets (circulation of oxygenated haemolymph first to brain and active tissues, followed by delivery of spent haemolymph to the gills and specific features to prevent admixture or oxygenated and deoxygenated haemolymph) are equally relevant here.

Before proceeding to advanced crustaceans, I want to focus briefly on the blood vascular system in a uniramian arthropod, the scutigeromorph centipede *Scutigera* sp., depicted in Fig. 5. Most uniramians exhibit only the simplest of circulatory systems with only a single dorsal heart, as described above and
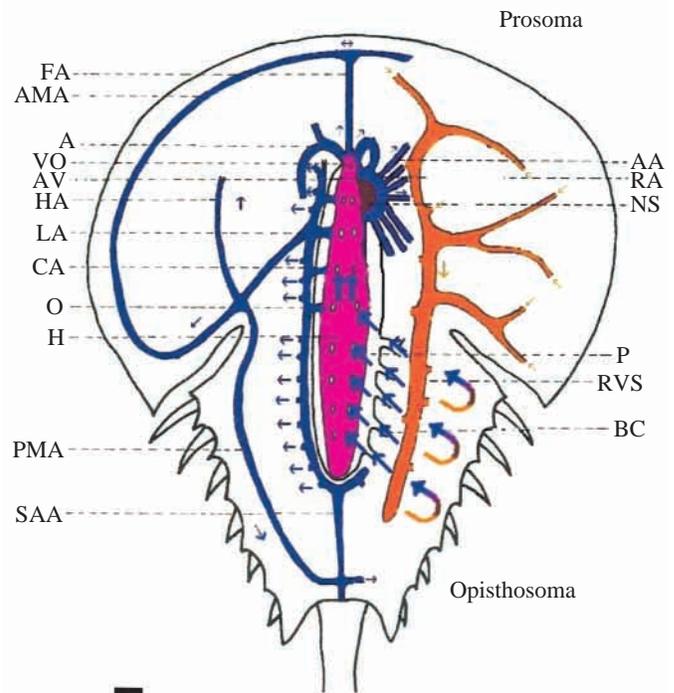

Fig. 4. An explanatory diagram of the blood vascular system of *Limulus polyphemus*. A, anterior aorta; AA, anterior aortic ring vessels; AMA, anterior marginal artery; AV, aortic valve; BC, branchiocardiac canal; CA, collateral artery; FA, frontal artery; H, heart; HA, hepatic artery; LA, lateral artery; O, ostium; P, pericardium; PMA, posterior marginal artery; RVS, right venous collecting sinus; SAA, superior abdominal artery; VO, vestigial ostia. Scale bar, 1 cm. Blue shading indicates the arterial distribution system; orange shading indicates the ventral venous return pathway. Arrows indicate the direction of haemolymph flow. Transition (orange→blue arrows indicate oxygenation in the gill books. Red indicates the heart. (Redrawn, with additional detail added, from Redmond et al., 1982.)
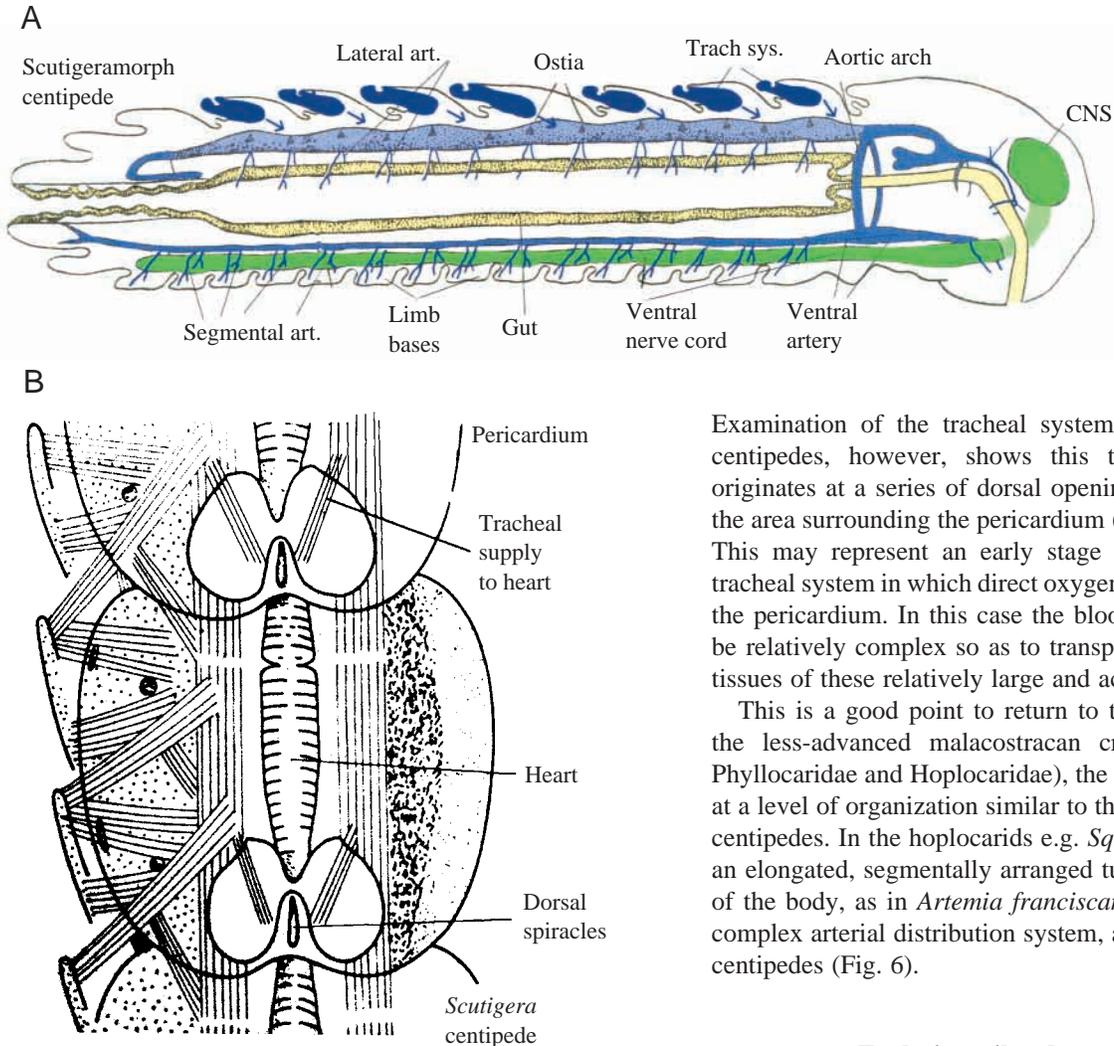
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Fig. 5. (A) Diagram of the blood vascular system of a generalized scutigeromorph centipede. Dark blue shading represents the location of the dorsal tracheal system; light blue represents the heart and vascular system; green shading indicates the central nervous system; yellow shading indicates the alimentary canal. Arrows indicate passage of oxygen through the tracheal system to the haemolymph in the pericardium. CNS, central nervous system. a, art., arteries; sys., system. (Modified from Beklemishev, 1969.) (B) Diagrammatic dorsal view of several segments of *Scutigera* sp. to show the tracheal system supplying only the pericardium and heart. (Taken from Minelli, 1993, with permission.)

typified by most insects. In many centipedes, however, the blood vascular system is highly complex with well-developed interconnected dorsal and ventral arterial distribution systems supplying segmental viscera and appendages, respectively. This system is very similar in organization and complexity to that of many crustacean systems (see Fig. 6). That this system is found within the Uniramia is initially surprising since this largely terrestrial group is typified by a well-developed tracheal system, which delivers oxygen directly to the cellular level thus obviating the need for a complex arterial system.

Examination of the tracheal system of the scutigeromorph centipedes, however, shows this to be quite unique. It originates at a series of dorsal openings and ramifies only in the area surrounding the pericardium (Fig. 5B; Minelli, 1993). This may represent an early stage in the evolution of the tracheal system in which direct oxygenation occurs only within the pericardium. In this case the blood vascular system must be relatively complex so as to transport O_2 effectively to the tissues of these relatively large and active centipedes.

This is a good point to return to the crustaceans since, in the less-advanced malacostracan crustaceans (e.g. in the Phyllocaridae and Hoplocaridae), the blood vascular system is at a level of organization similar to that in the scutigeromorph centipedes. In the hoplocarids e.g. *Squilla* sp. the heart is still an elongated, segmentally arranged tube extending over most of the body, as in *Artemia franciscana,* but with a relatively complex arterial distribution system, as in the scutigeromorph centipedes (Fig. 6).

Evolutionarily advanced systems

In many simple crustaceans, most segments bear unspecialized phyllopod appendages that function primarily in filter-feeding and/or locomotion but which also function in gas exchange via thin-walled gill extensions. During the evolution of the malacostracan crustaceans, structural and functional specialization of the limbs has occurred, with the result that respiratory structures that occurred ancestrally on most appendages have become (i) localized to specialized regions and (ii) correspondingly more complex, with a greatly increased surface area. To ensure functional efficiency of respiratory gas transport, these changes were necessarily accompanied by modification of the blood vascular system, which maintained efficiency of respiratory gas transport (i.e. followed the three basic tenets outlined above). Delivery of oxygenated haemolymph to the cephalic nervous system and sensory structures occurs by a large anterior aorta supplying the area. Perfusion of the cephalic ganglion has not been described and, for the moment, it may be assumed that haemolymph superfuses the ganglion as in *Artemia franciscana*. In these early malacostracan crustaceans the supply of oxygenated haemolymph to tissues still occurs primarily through two series of segmental arteries, the first
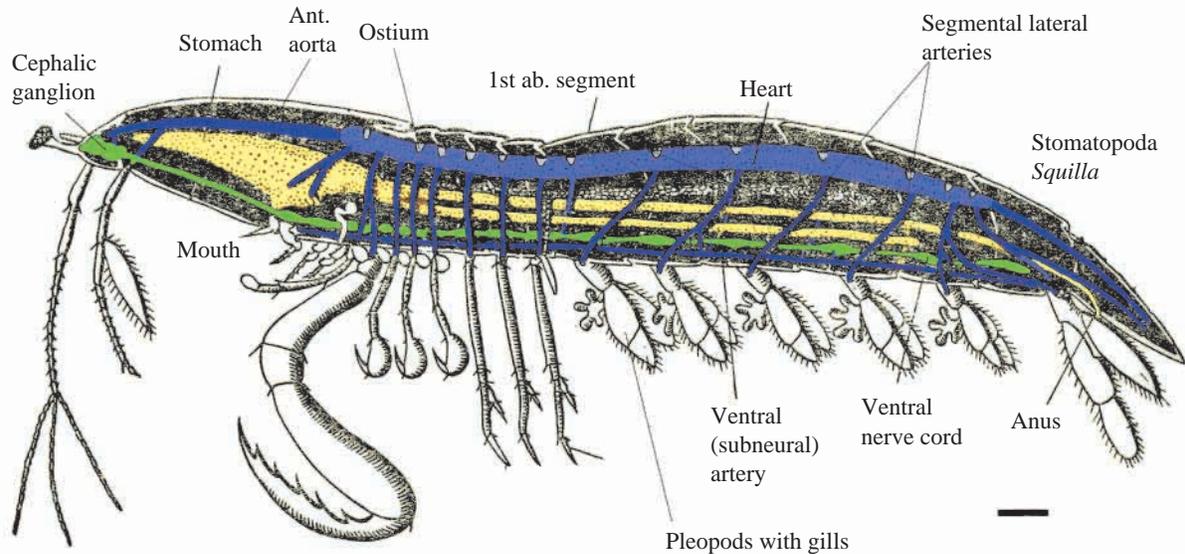
Fig. 6. Diagram of blood vascular system of *Squilla sp.* Blue shading represents the heart and vascular system; green shading indicates the central nervous system; yellow shading indicates the alimentary canal. Ant., anterior; Ab., abdominal. Scale bar, 1 cm. (Modified from Beklemishev, 1969.)

leaving the dorsal vessel (heart) to supply the viscera, the second leaving the ventral aorta to supply segmental appendages. In *Squilla*, however, unlike the situation described for scutigeromorph centipedes, there is extensive segmental interconnection between the dorsal and ventral arteries (Fig. 6).

In most malacostracan crustaceans, admixture of oxygenated and deoxgenated haemolymph is minimized since input to the heart via the ostial valves occurs principally in areas where there is an oxygenated supply of hæmolymph to the pericardium (McLaughlin, 1983). In *Squilla* sp., which are considered to represent a fairly primitive malacostracan condition, complex filamentous gills occur in five abdominal segments (Fig. 6). Deoxygenated haemolymph is collected via a large ventral lacuna and passes directly to the gills, from which reoxygenated haemolymph passes via dorsally directed sinuses directly to the pericardium through segmental ostia into the posterior heart. Ostial inputs also occur in several non-gill-

bearing segments, but since the return of deoxygenated haemolymph to this area has not been described, admixture of oxy- and deoxygenated haemolymph may be assumed to be minimal.

With the increased specialization of the gas-exchange regions and greatly increased condensation of the heart seen in the decapod crustaceans (Figs 1, 7) the segmental distribution of oxygenated haemolymph from the heart to the body is greatly reduced, leaving relatively few arteries now supplying large regions of the animal. Wilkens and coworkers (Wilkens, 1997; Wilkens et al., 1997) show that although the muscular pumping region (or heart) becomes highly condensed within the cephalothorax, the posterior aorta retains the ancestral function, supplying the abdominal musculature by means of segmental lateral arteries. In contrast to the situation in the other blood vascular systems described so far, decapod crustaceans have only a single vessel, the large sternal artery, connecting the heart and ventral vessel. Arterial output from
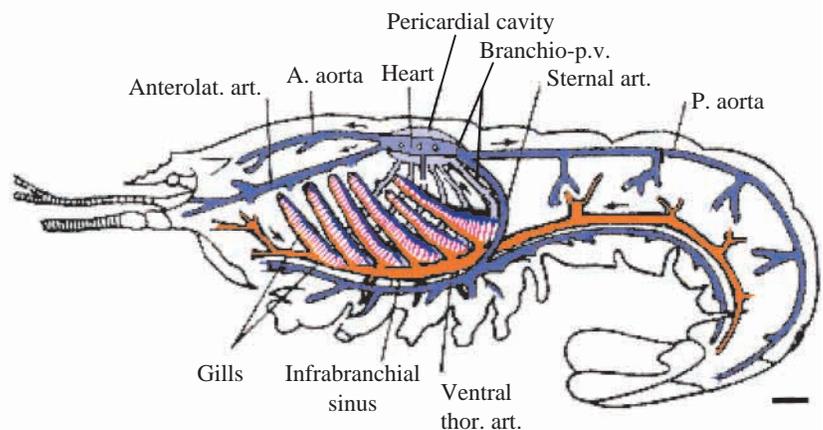

Fig. 7. Diagram of flow through the blood vascular system of a decapod crustacean (lobster). Blue shading indicates the heart and arterial distribution system. Orange shading indicates the ventral venous return pathway. Transitional (pink) shading indicates oxygenation in the gills. Anterolat., anterolateral; thor., thoracic; art., artery; A., anterior; P., posterior; p.v., pericardial veins. (Modified from Beklemishev, 1969.) Scale bar, 1 cm.

the ventral vessel also remains essentially segmental, supplying the appendages in each segment. As in other crustaceans, deoxygenated haemolymph returning from active tissues collects in a pair of large infrabranchial sinuses, which distribute haemolymph to an elaborate series of paired gills. Oxygenated haemolymph from the gills passes through specific channels, termed branchio–pericardial veins, to the pericardium surrounding the heart. Thus, as in other higher crustaceans, cardiac input occurs only in regions that collect oxygenated hæmolymph, preventing any admixing of oxygenated and deoxygenated hæmolymph.

Decapod crustaceans also show advances in the oxygenation of the central nervous system which, in both the crab *Carcinus maenas* and in crayfish, occurs by internal perfusion through a complex system of distribution sinuses (Sandeman, 1967; McMahon et al., 1997) rather than by superfusion as in other groups. Sandeman also demonstrates highly complex perfusion of the optic lobes in *Carcinus maenas* (Sandeman, 1967). Haemolymph perfusion of the central nervous system has been very poorly studied in arthropods generally, but a report of perfusion of the cephalic ganglion of a cephalocaridan *Hutchinsoniella macracantha* (Elofsson and Telford, 1992) is of interest. Since the Cephalocarida are generally regarded as representing the most primitive group this may be an ancestral crustacean character.

Functioning and control of decapod crustacean hearts

A new factor influencing controlled distribution of oxygenated hæmolymph arises with the adoption of a highly condensed heart. Segmental arterial distribution systems are substantially reduced, and oxygen delivery to the viscera, in particular, becomes a function of a few specialized arterial distribution systems that supply major body regions (Fig. 7). In decapod and isopod crustaceans, and in many other arthropods, including *Limulus polyphemus* (Redmond et al., 1982) and the scorpions and some spiders ((Farley, 1985; Paul et al., 1994), vessels leaving the heart are equipped with complex semi-lunar valves (Fig. 8; McMahon et al., 1997). These cardioarterial valves contain innervated muscle (Alexandrowicz, 1932; Kuramoto and Ebara, 1984; Kihara and Kuwasawa, 1984) and can be caused to contract progressively by either neural or neurohormonal stimulation so as to restrict cardiac outflow into that particular vessel. Since the valves of particular arterial systems are innervated separately this provides a mechanism by which the outflow of the heart can be diverted into particular arterial systems and thus to particular body regions.

Since these valves are present in such a wide range of arthropods we may assume that they represent an ancient feature. If present in the earliest, segmentally organized, circulatory systems, their function might have been to divert haemolymph flow to locomotor or visceral circuits within each segment

The functioning of extant cardioarterial valves is best understood in decapod and isopod crustaceans (see McMahon
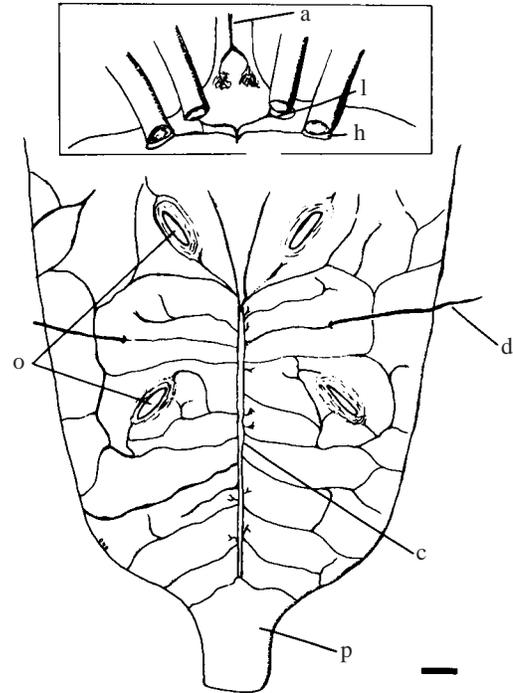

Fig. 8. Diagram of heart of lobster to show ostia and arterial valves and nervous connections. a, nerve to anterior arterial valve; c, cardiac ganglion; d, dorsal nerve to heart; h, hepatic arterial valve; l, lateral arterial valve; o, ostial valves; p, posterior aorta. Scale bar, 1 mm. (Taken from McMahon, 1998, with permission.)

et al., 1997, for a review). Each arterial system now supplies a functional region of the body (Fig. 7), and it is clearly important that oxygenation of each region be separately controlled. An example of circulatory control systems in action is seen in the work of DeWachter and McMahon (DeWachter and McMahon, 1996). These authors exercised individual Dungeness crabs *(Cancer magister)* non-stressfully using a rotating treadmill, on which the crabs walked slowly but continuously, to remain in a shaded preferred location. Each animal was fitted with pulsed-Doppler flow transducers that recorded flow through each arterial system simultaneously. During this slow sustained walking activity cardiac output increased, largely by an increase in cardiac stroke volume (Fig. 9A). The increased cardiac outflow, however, is not distributed equally among the vascular circuits; instead hæmolymph flow ceases in the hepatic arterial system leading to alimentary structures and increases in the sternal artery leading to the limbs (Fig. 9B). This indicates that, during activity, the increased cardiac output is diverted away from digestive structures and delivered preferentially to the limbs and gills. In other words, oxygen and nutrients are diverted to essential systems, precisely as occurs in mammals (reviewed in Guyton, 1996). Restitution of resting flow patterns occurs on cessation of activity. Similar shunting of haemolymph away from visceral structures and towards the limbs and gills also occurs in crustaceans exposed to hypoxia (Airriess and McMahon, 1994; B. R. McMahon, manuscript in preparation).
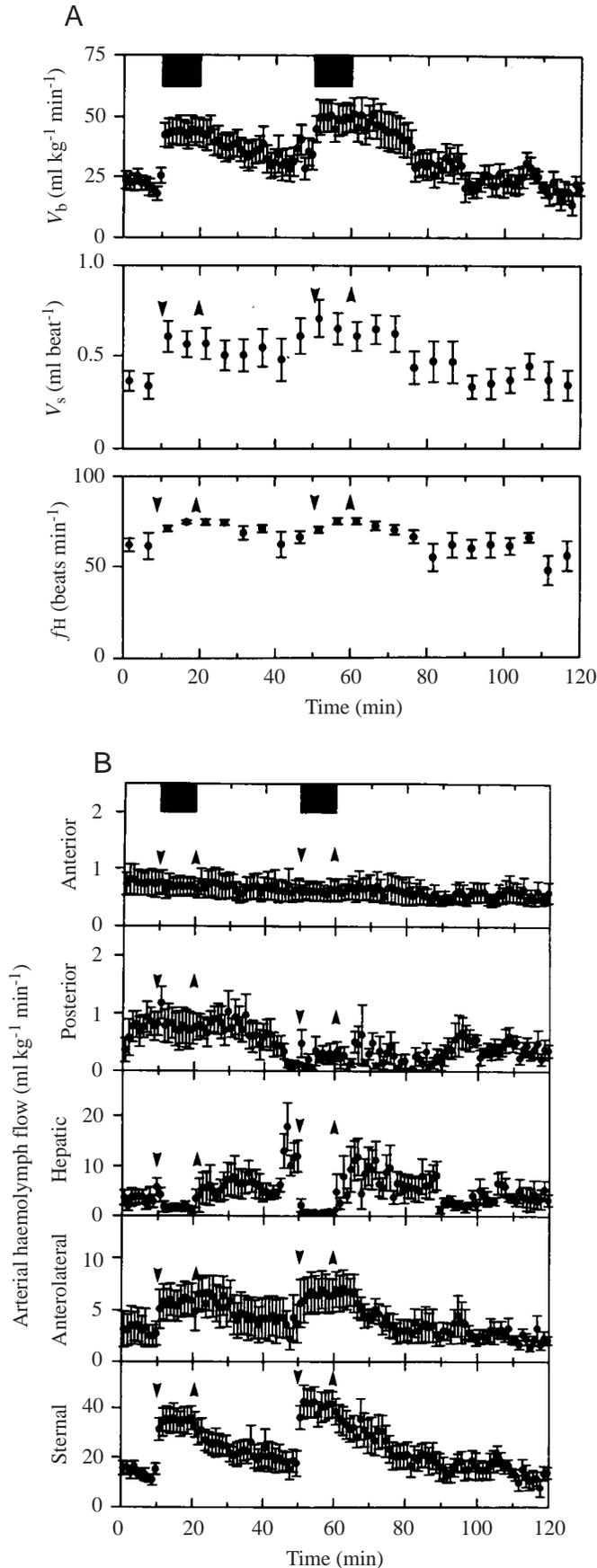
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Fig. 9. (A) Cardiac responses during two periods of slow walking in the Dungeness crab *Cancer magister*. Lower trace: f_H, heart rate in beats min^{-1}. Middle trace: V_s, heart stroke volume in ml beat^{-1}. Upper trace: V_b, cardiac output in ml kg^{-1} min^{-1}. Values are means ± S.E.M. Active periods are indicated by black bars at the top and by arrowheads within each trace. (B) Vascular responses during two periods of slow walking in the Dungeness crab *Cancer magister*. Each point represents haemolymph flow within the labeled arterial system (means ± S.E.M.). Active periods are indicated by black bars at the top and by arrowheads within each trace. (Modified from DeWachter and McMahon, 1996.)

Control mechanisms for these circulatory responses are not fully elucidated but a considerable body of recent work *in vitro* indicates that many aminergic and peptidergic hormones have effects both on the isolated heart and cardioarterial valves, and on the scaphognathites (Kihara et al., 1985; Kuramoto et al., 1992; Wilkens et al., 1996). These studies clearly indicate that changes in circulating amine levels could play a role in the control of decapod cardiovascular systems. We must, however, be careful in the interpretation of the results of these *in vitro* studies since the results of the few *in vivo* (whole animal) studies often show effects markedly different from those reported for the isolated heart (McGaw et al., 1995). This presumably arises since hormones added *in vitro* can have many additional effects on the heart and arterial valves, pericardial organs, etc. via sequential actions on different neural systems activated as the hormone perfuses the cephalic and ventral central nervous system. The effects of pericardial infusion of the crustacean peptide hormone proctolin *in vivo*, for instance, include an increase in cardiac output and shunting of haemolymph into the sternal artery (Fig. 10; McGaw et al., 1994) and, although not proven, it is tempting to speculate that changes in the concentrations of this hormone might be involved in the responses to hypoxia and activity described above. Infusion of crustacean cardioactive peptide (CCAP) has the opposite effect, diverting flow to the anterior vessels and away from the posterior ventral axis, while infusion of octopamine increases flow through the anterior aorta alone (Airriess and McMahon, 1992). These hormones are known to be present in the pericardial organs and can be released into the haemolymph stream immediately before entry into the heart. Thus it appears possible that differential release of peptidergic and/or aminergic hormones could act to mediate these cardiovascular responses either directly or indirectly via their actions within the central nervous system.

Equally, neural mechanisms may play a role. Wilkens and Walker (Wilkens and Walker, 1992) demonstrated the strong effects of stimulation of cardioexcitatory and cardioinhibitory nerves on heart frequency in crayfish. Guirguis and Wilkens (Guirguis and Wilkens, 1995) and Rose et al. (Rose et al., 2000) demonstrate that the nerve supply to the heart is essential for the rapid increase heart rate seen at the onset of activity in walking lobsters. In addition, neural stimulation may induce release of cardioactive hormones stored in the pericardial organs. Much research in this area is needed before the control mechanisms involved are fully understood.
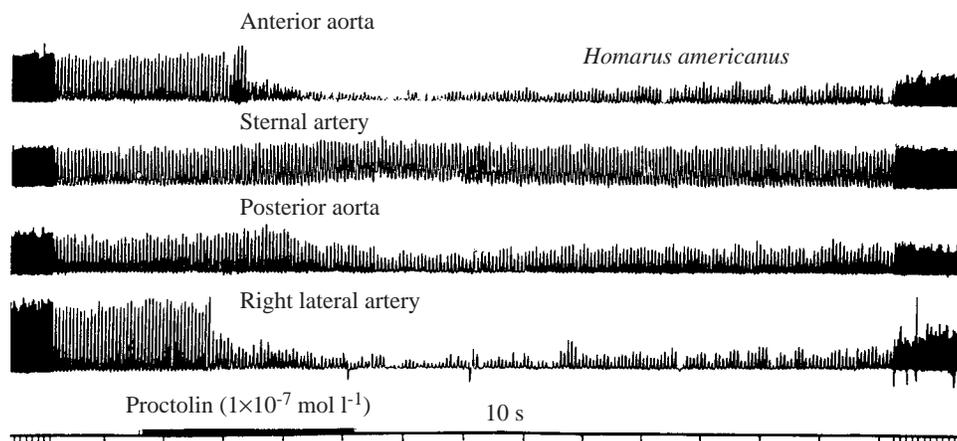
Fig. 10. Haemolymph flow velocity recordings in the anterior aorta, posterior aorta and sternal and lateral arteries of the lobster *(Homarus americanus)* showing the effects of an infusion of 10^{-7} mol l^{-1} Proctolin into the pericardial cavity. (Taken from McMahon, 1992, with permission.)

Interesting changes in cardiovascular control mechanisms also occur during ontogeny in the shrimp *Metapenaeus ensis* (Doyle and McMahon, 1997). In this decapod the excitation of the larval heart is initially myogenic but a transition to the neurogenic control typical of adults occurs in mid juvenile life. A similar transition occurs during development of the isopod *Ligia oceanica* (Yamagishi and Hirose, 1997). In *Metapenaeus ensis* cardiac responses to a variety of stimuli, including neurohormones such as 5-hydroxytryptamine (B. R. McMahon et al., manuscript in preparation) and environmental factors (e.g. hypoxia; McMahon et al., 1995), are strongly altered, often reversed, during juvenile development. This suggests that the relative importance of the circulatory system in gas exchange and nutrient supply to the tissues differs in larval stages and small juveniles from that occurring in the adult and that this is reflected in major differences in both responses and in control mechanisms.

The material reviewed here provides an opportunity to re-examine the functional evolution of the crustacean and arthropod circulatory and control systems. The occurrence of complex arterial distribution systems in widely separated arthropod groups indicates that the ancestral arthropod circulatory system was highly segmentally organized and probably of equivalent complexity to those of many polychaete annelids, differing largely only in the loss of vessel walls on the venous return pathways. The simple systems seen now in many smaller crustaceans represent a reduction in complexity due to the short diffusion path needed to serve the respiratory needs of the tissues.

With the invasion of the terrestrial habitat, many arthropod groups evolved a tracheal system that allowed molecular oxygen to be distributed directly to the cellular level and thus freed the circulatory system from its role in respiratory gas transport, again allowing reduction in complexity. Interesting intermediary conditions are seen in the Scutigeromorph centipedes in which the tracheal system penetrates only to the level of the heart and pericardial cavity, leaving the circulatory system to deliver the oxygen internally. More complex distribution systems also occur occasionally in the Insecta.

In conclusion, we have seen that the necessity for oxygen delivery to the nervous system and other active tissues is the predominant influence in cardiovascular control mechanisms of current decapod crustaceans and has played a major controlling role in the evolution of the arthropod circulatory system.

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