

# Chapter 2

## The Circulatory System of Spiders

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### 2.1 Introduction

Spiders are a fascinating group of animals which exhibit a range of different lifestyles. Despite this variety, however, the spider body is fairly uniform, consisting of a prosoma which mainly serves sensory and locomotory functions and an opisthosoma which mainly serves the remaining vegetative functions. As of the main organ systems, the circulatory system is greatly affected by this bipartition. Although its importance in homeostasis, immune defense, transportation, and hydraulics is known, our understanding of this integrative organ system is still in the early stages. In the following chapter the main structural and functional aspects of the circulatory system are reviewed.

### 2.2 Comparative Morphology of the Circulatory Organs

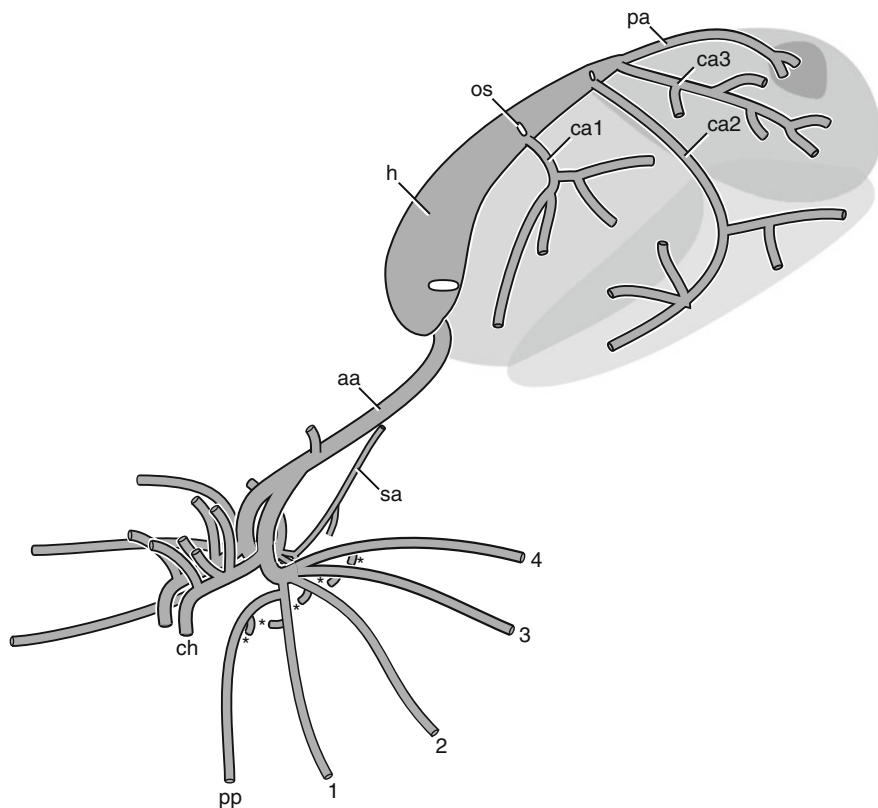
Spiders exhibit an open circulatory system made up of the hemolymph vascular system in combination with a complex system of sinuses and lacunae (hemolymph lacunar system). The hemolymph vascular system is composed of the central pumping organ, the heart, and arteries which emanate from it and open out into the hemolymph lacunar system (Wirkner and Richter 2010).

The tubular heart (h; Fig. 2.1) lies dorso-medially in the anterior part of the opisthosoma within a pericardial sinus. It curves convexly in line with the shape of the anterior opisthosoma. The unpaired anterior aorta emanates from the anterior end of the heart and runs through the pedicel to supply the entire prosoma (aa; Fig. 2.1). Posteriorly, the heart narrows and passes into the posterior aorta

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**Fig. 2.1** Schematic representation of the main structures of the hemolymph vascular system of a spider. Abbreviations see text

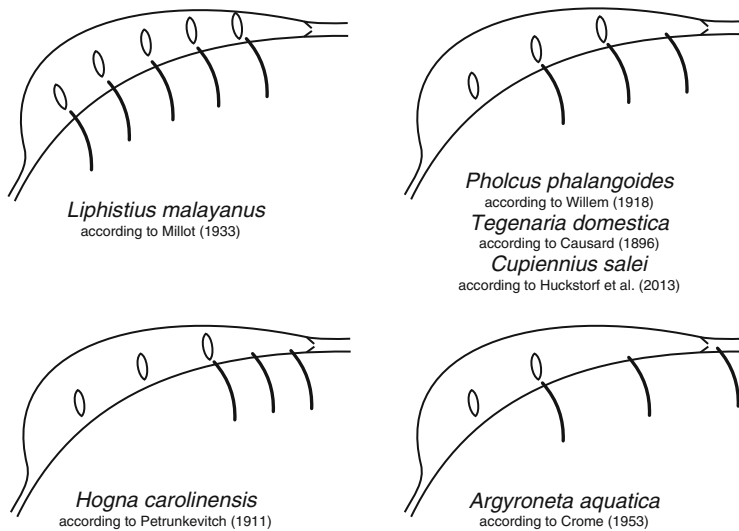
(pa; Fig. 2.1). The heart wall is made up of a thin outer layer, the epicardium, and a thick muscle layer, the myocardium. The muscle layer is comprised of cardiomyocytes which form lunated lamellae that are positioned transversely to the longitudinal axis and project deeply into the lumen of the heart (Seitz 1972; Huckstorf et al. 2013). In the dorsal and ventral part of the heart the lamellae interconnect alternately. Also embedded within the transverse muscle layer are longitudinal muscle bands. The heart is completely surrounded by a pericardial sinus and is suspended via dorsal, ventral, and lateral ligaments which fan out before fusing with the outer layer of the heart. Four (Mygalomorphae, Mesothelae, Palaeocribellatae, and some Austrochiloidea) or two pulmo-pericardial sinuses (remaining Austrochiloidea, Araneoclada) connect the pericardial sinus with the book lungs, enabling oxygen-enriched hemolymph to travel from the book lungs into the pericardial sinus (see also Burmester 2013 and Appendix, this volume). These sinuses have often misleadingly been termed “lung veins” although they do not form vessels directly connected to the hemolymph vascular system.

**Fig. 2.2** Micro-computed tomography of a resin cast of the hemolymph vascular system in the opisthosoma of *Cupiennius salei*. Note that only resin filling the arteries is visualized. Modified after Huckstorf et al. (2013). Compare Fig. 2.1



In addition to the anterior and posterior aortae, paired cardiac arteries emanate ventrolaterally from the heart, ramifying strongly to supply all parts of the opisthosoma (ca; Fig. 2.1). The liphistiid *Liphistius malayanus* displays the highest number of cardiac arteries with five pairs (Millot 1933). A stepwise reduction in pairs down to three (e.g., in the ctenid *Cupiennius salei*; Huckstorf et al. 2013) and two (e.g., the cybaeid *Argyroneta aquatica*; Crome 1953) occurred within derived spiders. It was recently possible in *C. salei* to visualize the entire arterial system of the opisthosoma (Fig. 2.2; Huckstorf et al. 2013). The antero-dorsal part of the opisthosoma is supplied by the anterior-most pair of cardiac arteries (ca1; Fig. 2.1), which ramifies just beyond its origin. The middle pair of cardiac arteries (ca2; Fig. 2.1) supply the greater portion of the ventral part of the opisthosoma, i.e. the gonads, spinning glands, and parts of the midgut. After emanating from the heart, they run a long distance ventrally before bifurcating into two strong branches each. The anterior branch runs in an antero-median direction and splits several times. The posterior pair of cardiac arteries (ca3) runs postero-ventrally into the anal region and supplies the postero-dorsal part of the opisthosoma.

The heart is equipped with slit-like openings, the ostia, through which the hemolymph can enter the lumen of the heart (os; Fig. 2.1). Ostia are formed by specialized cardiomyocytes which form lips that can close during systole to prevent hemolymph from flowing out of the heart. As a result of reduction in some spider lineages, the number of pairs of ostia varies (Fig. 2.3). The plesiomorphic state is five pairs as found in liphistiids (e.g. *L. malayanus*). This number was reduced to four in mygalomorphs (e.g., the theraphosid *Aphonopelma hentzi*, often mentioned sub *Eurypelma californicum*, Nentwig 2012) and basal araneomorphs (e.g., the austrochilid *Austrochilus* sp.), then three (e.g., the filistatid *Filistata hibernalis*; also basal araneomorphs). Within higher spiders a reduction down to two pairs is evident in several groups (Petrunkevitch 1933).



**Fig. 2.3** Schematic representation of various spider hearts showing the position of pairs of cardiac arteries and pairs of ostia. Modified after Huckstorf et al. (2013)

The anterior aorta and its branches supply the entire prosoma. From the anterior tip of the heart the anterior aorta runs through the pedicel into the prosoma (aa; Fig. 2.1). It divides into two branches just posterior to the sucking stomach. Flanking the stomach laterally, these two branches run in an anterior direction and give off several small arteries.

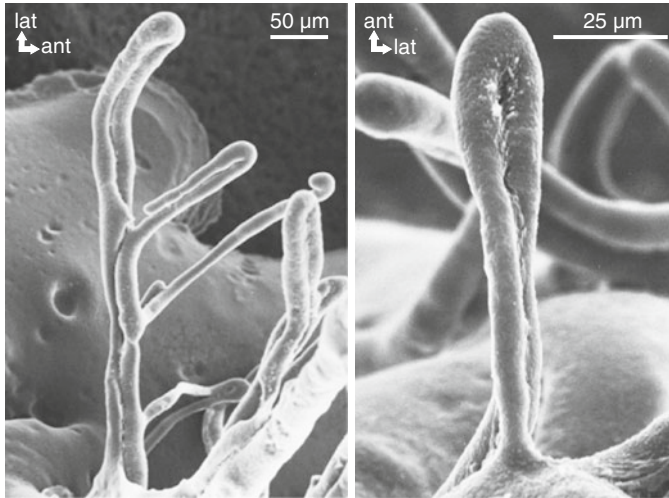
Above the subesophageal ganglion, each branch of the anterior aorta bends in a ventral direction to rest on the dorsal side of the subesophageal ganglion. At this bend, one cheliceral artery branches off each aortic branch and runs in an anterior direction, flanking the supraesophageal ganglion dorsolaterally. On their way into the chelicerae the cheliceral arteries (ch; Fig. 2.1) give rise to several other arteries, some of which supply the supraesophageal ganglion. Two pairs of these latter arteries are present in the agelenids *Tegenaria* sp. (Schneider 1892) and *Agelena labyrinthica* (Causard 1896) while in *Cupiennius salei* three pairs occur (Huckstorf et al. 2013). Furthermore, dorsal branches emanating from the cheliceral arteries supply the dorsal musculature of the anterior prosoma. The optical arteries, which also arise from the cheliceral arteries, run dorsally to the eyes and branch repeatedly. The supply of the upper and lower lips varies between spider taxa. In most spiders a branch of the cheliceral arteries supplies the upper and lower lips together (e.g., *Tegenaria* sp.; Schneider 1892). In others, the upper and lower lips are each supplied by arteries which split off from the cheliceral arteries. In *Araneus diadematus*, an artery emanating from the anterior aorta supplies the lower lip (Schneider 1892; Runge and Wirkner, unpublished data). In addition, the cheliceral arteries give off dorsolateral branches to supply the venom glands and the dorsolateral muscles of the anterior prosoma. The cheliceral arteries then run ventrally into the chelicerae, where a number of small arteries branch off.

After having bent, the branches of the anterior aorta run ventrally to form an arch along the dorsal side of the prosomal ganglion. It is from these arches that the arteries for the four pairs of legs emanate (1–4; Fig. 2.1). The pedipalpal arteries either branch off proximally from the arteries supplying the first leg (e.g., *Cupiennius salei*; Huckstorf et al. 2013; pp; Fig. 2.1) or from the branches of the anterior aorta directly (e.g., *Agelena labyrinthica*; Causard 1896; *Argyroneta aquatica*; Crome 1953). The coxae of the pedipalps are supplied by a ventro-anterior branch off the pedipalpal artery. Several small arteries emanate from the leg arteries on their way into the legs. The branches of the anterior aorta are interconnected via several small arteries just above the subesophageal ganglion (connecting arteries). The number of connecting arteries varies between and within spider taxa. The last connecting artery gives rise to the unpaired supraneural artery, which extends above the opisthosomal nerve to the pedicel (sa; Fig. 2.1).

The central nervous system, i.e. the supraesophageal ganglion (brain) and the subesophageal ganglion, is well supplied by vessels (for a review of central nervous system architecture in *Cupiennius salei*, see Seyfarth 2002; Barth 2002). This is achieved by a number of smaller vessels permeating the nerve mass after having branched off the main arteries in the prosoma. The subesophageal neuromeres are supplied medially by unpaired transganglionic arteries and laterally by paired arteries. The latter branch off from the leg and pedipalpal arteries. On each side, one artery emanates from the proximal end of each appendage artery and runs in an antero-ventral direction into the septum between two neighboring neuromeres (\*; Fig. 2.1). The septum between the cheliceral and pedipalpal neuromeres is supplied by an artery which branches off the pedipalpal artery. The transganglionic arteries take their origin from the connecting arteries and the proximal part of the supraneural artery. They run through the subesophageal ganglion from the dorsal to the ventral side. From the transganglionic arteries, a number of fine arteries extend into neighboring neuromeres, which they penetrate to over a third of their width. The center of the neuromeres remains largely free of arteries.

Although the vascularization of the central nervous system has long been the object of investigation (e.g., Schneider 1892), it is best understood in *Cupiennius salei* (Huckstorf et al. 2013) where it has been described as a form of capillarization in which supply is provided by a system of afferent and efferent vessels. A similar system of irrigation of the central nervous system is also found in crustaceans (Sandemann 1967; Abbott 1971; Brown and Sherwood 1981). In both crustaceans and spiders, certain areas of the central nervous system seem to be better supplied than others. In *C. salei*, these include the arcuate body and the third optic neuropil of the brain, which are especially rich in synaptic contacts. Hemolymph vessels and loops in the subesophageal ganglion (Fig. 2.4) ensure that supply to the peripheral layers of each neuromere is particularly abundant.

These are the regions where the majority of the neuronal somata are situated and where metabolic activity is high. Along the subesophageal midline, areas with a high oxygen requirement—those with dense synaptic contacts in which intense neuronal activity takes place—are also well supplied. Immunohistochemical studies have shown that octopamine- and serotonin-immunoreactive neurons project



**Fig. 2.4** Electron micrograph of a resin cast in *Cupiennius salei* showing loops supplying neuropiles in the subesophageal ganglion. Modified after Huckstorf et al. (2013)

into the close vicinity of hemolymph vessels in the subesophageal neuromeres, suggesting that these neuroactive substances are released into the hemolymph here to supply more peripheral organs (Seyfarth et al. 1990, 1993).

## 2.3 Functional Morphology of the Circulatory System

On the whole, the circulatory system in spiders has not been studied extensively. Although some aspects (e.g., hydraulic leg movement) are well explored, comparative morphological and functional studies are scarce, with the latter remaining fairly superficial and focusing on the relatively large and thus more easily accessible mygalomorph spiders. The following passages on functional morphology and physiology are therefore based on these few studies.

### 2.3.1 The Split/Bipartitioned Body

Paul et al. (1989) came up with a hydraulic model for explaining major body functions in spiders. After this model, the spider body can be described as being partitioned into two functional units, an anterior and a posterior region. In the latter, the vegetative/ visceral region, i.e. the opisthosoma, the main parts of the circulatory, respiratory, excretory, and reproductive organs are situated, while the anterior region, the prosoma, houses the main sensory and locomotory functions (apart from

food uptake and defense). The regions are connected by the rather thin pedicel, which drastically limits the exchange of body fluids. In terms of function, the two groups of organs display quite different time patterns. Vegetative systems have to perform to the needs of the whole animal/body. They work relatively continuously and have comparatively slow reaction times. Sensory and locomotory functions, on the other hand, require much faster reaction times. In accordance with its vegetative function, the opisthosoma displays long-term volume changes (degree of hydration, nutritional condition, degree of fertility/maturity, etc.), while in the prosoma, except for short-term changes during locomotion, a constant volume is maintained. The relative stiffness of the exoskeleton also reflects this division of physiological functions. The comparatively soft opisthosoma is—to differing degrees—expandable. The prosoma, on the other hand, is fairly rigid, providing the mechanical strength required for both the mechanical (muscular) locomotion system and the peculiar hydraulic system (see Kropf 2013) serving leg extension. The bipartitioning of the body is therefore of double advantage in this regard. On the one hand, only half of the body's cuticle requires reinforcement, and on the other, as this is the same half which necessitates higher internal pressure levels, the effort needed to build up this pressure can be greatly reduced. In terms of the vascular system, however, the partitioning poses a major challenge. First of all, despite differences in the level of supply required by the prosoma and the opisthosoma according to their different functions, hemolymph must be supplied to both regions. The mechanisms behind this shifting of hemolymph supply according to the requirements of the animal and vegetative regions are still not properly understood. A further complication is caused by differences in the configuration of respiratory organs. In species with more than one pair of lungs the contribution of each lung pair to the reoxygenation of the hemolymph and the release of carbon dioxide must be different to that with a complex tracheal system. There also seem to be more obvious “problems” with the bipartition of the spider body. First of all, the pumping action of the heart into the prosoma has to operate against the prosomal pressure generated during leg extension. This might in some cases lead to a severe lack of oxygen supply to the anterior body region, resulting in the complete exhaustion of the spider. In summary it should be clear that the circulatory system in spiders has to compromise between a large number of different functional and structural limitations and requirements.

### ***2.3.2 The Circulatory Cycle***

As described above, hemolymph is distributed via a varying number of cardiac arteries and one unpaired posterior aorta into the opisthosoma and via an unpaired anterior aorta into the prosoma. The arteries end openly in the hemolymph lacunar system by means of which hemolymph irrigates the tissues and supplies them with oxygen, nutrients and various other molecules such as hormones. Oxygen-poor hemolymph is conducted through the book lungs and there replenished with oxygen



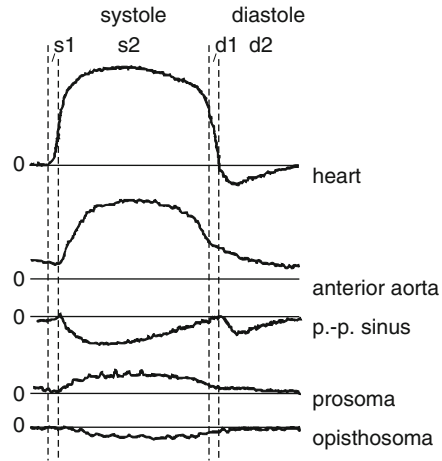
(Burmester 2013). Oxygen-rich hemolymph flows dorsally through the pulmo-pericardial sinuses into the pericardial sinus. Hemolymph reenters the lumen of the heart via the paired ostia. Measurements have shown, however, that hemolymph is unevenly distributed in the spider body, with the prosoma and opisthosoma not always receiving the same amount (Paul and Bihlmayer 1995). There are three possible ways in which this may be achieved. Firstly, the bidirectional movement of hemolymph could be caused by peristaltic heart contractions, as is known to be the case in insects (e.g., Pass 2000). In spiders, however, peristaltic contractions of this nature seem not to occur (at least not in *A. hentzi*; Paul and Bihlmayer 1995). Secondly, flow distribution may be controlled and regulated by arterial valves. In measurements again performed in *A. hentzi* (Paul and Bihlmayer 1995), the pressures in the anterior aorta and the heart were recorded to be the same, leading the authors to rule out this hypothesis. As arterial valve control has a strong influence on hemolymph distribution in some decapod crustaceans, however (e.g., McMahon and Burnett 1990), there is a strong case for it to be tested more comprehensively in spiders. Last but not least, changes in the resistance of peripheral vessels caused by a passive or active decrease in arterial diameters may also lead to an uneven distribution of hemolymph. Changes in resistance of this nature are known from decapod crustaceans, in which group they are mainly triggered by aminergic and peptidergic substances (McMahon et al. 1997), but spiders have not, as yet, been tested for such substances. The unevenness of the distribution of cardiac output also varies with in accordance with the activity level of the spider. On the basis of simultaneous measurements taken at a number of circulatory structures (e.g., the pulmo-pericardial sinuses and the anterior aorta), Paul and Bihlmayer (1995) were able to show that in *A. hentzi*, forward flow came to a halt during locomotion while flow in a posterior direction was kept up. Flow through both pairs of pulmo-pericardial sinuses was maintained during this phase. The opposite was measured shortly after locomotory activity. In some cases, changes in hemolymph flow direction were measured even during late recovery.

### 2.3.3 *The Cardiac Cycle*

The action of the muscular heart is the main motor of hemolymph movement. In arthropods, there are two basic ways in which the heart is activated to pump (Sherman and Pax 1968; Sherman 1985). Hearts which are stimulated by automatically beating myocardial cells are termed myogenic and occur in some crustaceans and hexapods (McMahon et al. 1997). Hearts which are mainly controlled by the central nervous system (though various other chemicals can provide additional stimulation) are termed neurogenic. One indicator of neurogenic control is the presence of nervous structures directly associated with the heart, i.e. cardiac ganglia and nerves. Cardiac nerves were first described in spiders by Wilson (1967), with Sherman and Pax (1969) later demonstrating their presence in a further 28 spider species. A cardiac ganglion lies on the mid-dorsal surface of the heart and extends



**Fig. 2.5** Pressure distribution in parts of the structures involved in circulation in *Aphonopelma hentzi*. Pressure baseline represents the noncardiac body pressure. Modified after Paul and Bihlmayer (1995)

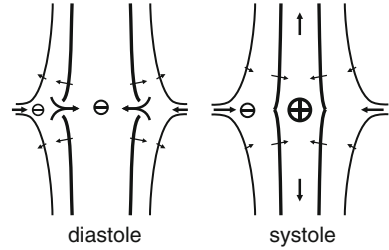


its entire length (Wilson 1967; Sherman and Pax 1968, 1969; Gonzalez-Fernandez and Sherman 1984), initiating and coordinating the heartbeat (Bursey and Sherman 1970) and sending out motor nerves which innervate the myocardial cells (Sherman 1973; Ude and Richter 1974). In *Aphonopelma marxi*, Gonzalez-Fernandez and Sherman (1984) actually demonstrated the presence in spiders of cardioregulatory nerves containing both inhibitory and acceleratory neurons (Gonzalez-Fernandez and Sherman 1984). Other studies involving pharmacological experiments all come to the conclusion that the basic form of heart control in spiders is neurogenic (Sherman and Pax 1970a, b; Martin 1974).

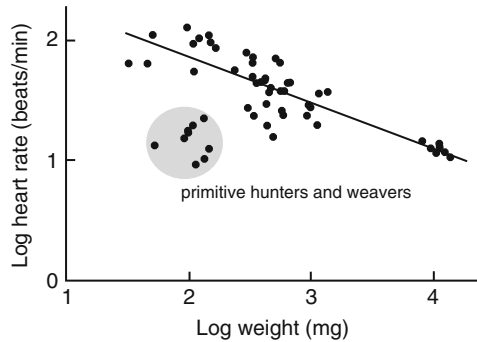
The movement of the heart can be divided into a phase of contraction, the systole, and a phase of relaxation, the diastole. Each of these phases can be again subdivided into two different phases (Paul and Bihlmayer 1995). In the first phase of the systole the myocardium contracts more or less isovolumetrically (Fig. 2.5) and no hemolymph flow occurs through the arterial systems. When pressure in heart surpasses pressures in the arteries, valves between the heart and the arteries are forced open and hemolymph is pumped into the arterial systems. In this first phase of the systole, pressure increase is rapid, then followed by a slow decrease (Fig. 2.5). After this, the myocardium relaxes slowly (the first phase of the diastole), resulting in a rapid decrease in hemolymph pressure to below that in the arterial systems and a closure of the arterial valves. In the second phase of diastole the pressure inside the heart becomes negative. During both the systole and the diastole, pressures inside the pulmo-pericardial sinuses are negative, allowing a continuous hemolymph flow to be kept up for the duration of the whole cardiac cycle (Paul and Bihlmayer 1995).

In mygalomorph spiders at least, the heart and the pericardial sinus act together as a pressure-suction-pump (Paul et al. 1994; Paul and Bihlmayer 1995). While the heart is suspended elastically, the pericardial membrane seems to be fairly fixed, which means that volume changes are significant but minor (Fig. 2.6a). Cardiac

**Fig. 2.6** Schematic functional representation of the pressure-suction pump in *Aphonopelma hentzi*. Pressures given for the pericardial sinus equal those in the pulmo-pericardial sinuses. Modified after Paul and Bihlmayer (1995)



**Fig. 2.7** Heart rate in spiders as a function of body weight. The regression line is indicated for all spiders except some hunters and weavers. Modified after Carrel and Heathcote (1976)



systole, i.e. the contraction of the myocardium, results in a change in volume in the pericardial sinus which affects a negative pressure which causes hemolymph to be sucked out of the pulmo-pericardial sinuses at the same time as it is pumped through the heart. The pressure remains negative in the pericardial sinus even during the diastole of the heart (Fig. 2.6b) because as the myocardium is widened through the action of the alary muscles and the pericardial membrane also moves back slightly into its original position, hemolymph continues to be sucked out of the pulmo-pericardial sinuses even as it is sucked into the heart.

### 2.3.4 Heart Rate

Carrel and Heathcote (1976) measured the resting heart beat in 18 species of spiders using a laser trans-illumination technique. All the animals were unrestrained and had no further equipment attached to their body. Heart rates ranged from 9 to 125 beats per minute. Resting heart rates correlate with body size and, except in the case of some hunting and orb-weaving spiders, with body weight (Fig. 2.7). Naturally, activity leads to an increase in heart beat frequency. Experiments carried out by Paul and Bihlmayer (1995) in *A. hentzi* showed that activity can cause the heart to beat up to ten times faster than in resting individuals, and that it takes more than 50 min for the frequency to drop down to resting values following activity. Similar

results were presented by Bristowe (1932) for *Liphistius desulator*. During a short burst of activity the heart rate in this spider went up to 120 beats per minute. In the first 5–10 min after this, a rapid decrease was observed, but it took more than 40 min for the resting heart beat of 48 beats per minute to be regained. Carrel (1987) reported on the various factors that can influence spider heart rate, listing, apart from activity, correlations with body size, metabolic rate and temperature and the effects of arthropod venoms such as those from wasps and millipedes. The reader is referred to that chapter for more detailed information on heart rate.

### 2.3.5 Hemolymph Pressures

The other main function of the circulatory system is the generation of blood—or in this case hemolymph pressure. The cardiac pressures generated in mygalomorphs at rest are relatively low: 1.2/0.8 kPa systolic/diastolic in *Aphonopelma* sp. (Stewart and Martin 1974) and 0.5–1.5/–0.1 kPa in *A. hentzi* (Paul et al. 1994; Paul and Bihlmayer 1995). Cardiac pressures can change in accordance with alertness, water uptake, and hemolymph loss. The pressure gradients that occur during rest are solely the result of the action of the heart-pericardial system, i.e. the pressure-suction pump. Paul and Bihlmayer (1995) discovered that in *A. hentzi* heart output, i.e. the volume pumped by the heart over a certain time interval, had the capacity to increase without an increase in heart beat frequency. The authors interpret this, on the basis of a series of experiments and measurements, as being the product of an increase in cardiac stroke volume. Apart from the heart there are two further hemolymph pressure generators in spiders. These are certain groups of prosomal and opisthosomal muscles, which, due to their contraction, produce a steady regime of above ambient pressure in the whole spider body (Wilson 1970; Anderson and Prestwich 1975; Paul and Bihlmayer 1995). All three hemolymph generating systems interact on various functional levels such as the hydraulic leg extension, etc. (Kropf 2013).

## 2.4 Conclusions

The spider circulatory system is a structurally complex and elaborately regulated system with a broad range of functionalities. Apart from its well-known role in metabolism and, plesiomorphically at least, in oxygen distribution, its main functions are hydraulic. Though we know much about the structure and function of this important organ system, it is highly desirable that comparative studies on both the morphological and functional/physiological levels be carried out to shed more light on the complex interactions of this system. The fact that Araneae are a monophyletic group makes them an ideal object to study the different pathways taken during the evolutionary development of this uniform yet uniquely diverse group of chelicerates.

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