

Respiration by jumping spiders (Araneae: Salticidae)¹

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Abstract. Functional morphology of the book lungs and tracheal systems of salticid spiders is reviewed and illustrated. Problems related to the ventilation of book lungs, use of spiracles to regulate discontinuous gas exchange, and the respective roles of book lungs and tracheae are discussed and compared to recent findings from the study of insect respiratory systems.

Keywords. air sac, book lung, *Colonus*, desiccation, diffusion gradient, discontinuous gas exchange cycle, heartbeat, hemolymph, hemolymph bellows hypothesis, hygric hypothesis, hypocardial ligaments, *Lysomanes*, oxygen toxicity, pericardium, *Phidippus*, rebreather, spiracle, trachea, ventilation

Jumping spiders can be very active creatures. We presently have little data bearing on the question of their peak requirements for the exchange of the CO₂ that they produce for the O₂ that they require. In the laboratory, Anderson (1968) reported that a very large salticid (*Phidippus regius* C. L. Koch 1846, ~560 mg) consumed ~120 µl O₂/hr in the daytime, and ~60 µl O₂/hr at night.

The respiratory system of a spider must do far more than obtain molecules of atmospheric O₂. It must also remove a similar number of the CO₂ molecules that are produced by its metabolism. Given the high concentration of O₂ in the atmosphere, diffusion of CO₂ from the hemolymph to the atmosphere is a much slower process than is diffusion of O₂ in the opposite direction. So a spider must also deal with fact that reliance on diffusion alone to remove excess CO₂ could also introduce far more O₂ than is needed, resulting in *oxygen toxicity*. All terrestrial animals must maintain a balance (*oxygen homeostasis*) between their supply of oxygen and its toxicity (Hsia et al. 2013).

For small arthropods we must add the universal problem of H₂O loss (Woods & Smith 2010). Without safeguards, an open exchange of gases between the hemolymph and the atmosphere would quickly desiccate the spider. Water must be protected, particularly in hot or arid climates. For arthropods, the presence of spiracles that can be closed is generally thought to limit water loss (Canals et al. 2015). The thin cuticle (~0.14 µm) of the book lungs of the spider *Grammostola rosea* (Walckenaer 1837) has been associated with 60% of its water loss (Canals et al. 2007, 2015). Figueroa et al. (2010) also reported that 60% of water loss by the spider *Paraphysa* was associated with the book lungs, and suggested that, as in insects, spiracles were closed to restrict water loss.

Salticid spiders have evolved two very-well developed respiratory systems to deal with these problems, both of which bring atmospheric gases very close (~0.16-0.19 µm) to body tissues for exchange [Schmitz & Perry 2000, 2001, *Salticus scenicus* (Clerck 1757)]. Like many other arachnids, including the related amblypygids, spiders have 1-2 pairs of book lungs that open through spiracles on the underside of segments VIII and IX (opisthosomal segments II and III) (Dunlop & Lamsdell 2017). Mygalomorphs have

two pairs of book lungs on segments VIII and IX, but no tracheae (Levi 1967; Reisinger et al. 1990; Canals et al. 2007; Brunelli et al. 2015). Some arachnids lack book lungs altogether. For example, solifugids have evolved an extensive system of air sacs and tracheae similar to those of insects (Franz-Guess et al. 2016). Salticids, like other entelegynes, possess a single pair of book lungs at segment VIII, and an extensive system of tracheae associated with a single spiracle located on segment IX (opisthosomal segment III), the latter in a medioventral position just anterior to the spinnerets (Figure 1; Appendix 1; see also Purcell 1909; Levi & Kerber 1976; Ramírez 2000; Schmitz 2013).



Figure 1. Ventral views of an adult female *Phidippus princeps* (Peckham & Peckham 1883) from Greenville County, South Carolina. **2,** Detail of ventral opisthosoma, showing (arrows) the two pulmonary spiracles on either side of the epigastric groove, and the single tracheal spiracle just in front of the articulated spinnerets. In front of each pulmonary spiracle the glabrous surface of the thick cuticular plate that covers the respective book lung, the *operculum*, can be seen, one on either side of the epigynum at the median. *Phidippus* females often have distinctive patterns like this on the underside of the opisthosoma. In *P. princeps*, the darker midventral area corresponds to the position of the large, branching air sac that extends anteriorly from the tracheal spiracle. For ventral views of more salticids see Appendix 1.

The reason that these spiders have two very different respiratory systems, the one (book lungs) closely associated with the heart and the transport of gases by circulating hemolymph containing hemocyanins (Schmitz & Perry 2000; Ballweber et al. 2002; Burmeister 2013), and the other (tracheae) bringing atmospheric gases directly to certain organs, is not fully understood. Book lungs are considered to represent the more primitive mode of respiration. This duality has definitely encouraged our creative speculation. Several writers (Kästner 1929; Opell 1998; Schmitz & Perry 2000) have noted that there is a trade-off in the development of the one system versus the other in the Araneae, although in salticids both are well-developed. Both systems appear to be necessary to support an active salticid, but either might

be sufficient during a period of low activity [Schmitz & Perry 2001, *Salticus scenicus*; Schmitz 2004, 2005, *Marpissa muscosa* (Clerck 1757)]. For salticids, tracheae are primarily associated with the digestive gland in the opisthosoma, and the central nervous system in the prosoma. This may support (1) a greater local demand for the exchange of gases by these tissues, particularly during periods of inactivity (Schmitz 2013; Hsia et al 2013). Other hypotheses used to explain the use of tracheae include (2) a general requirement for more O₂ during periods of activity, when hemolymph circulation may be interrupted by higher fluid pressure in the prosoma (Levi 1967; Levi & Kerber 1976; Schmitz & Perry 2000; Schmitz 2013; Hsia et al 2013), (3) a more general (not tissue-specific) need for more O₂ (Schmitz 2013; Hsia et al 2013), or (4) water conservation, particularly during periods of inactivity or aridity, which may be more effective for tracheae than for book lungs (Hill 1977a, 2008a; Schmitz & Perry 2000; Schmitz 2013; Hsia et al 2013). In support of (2), some spiders have tracheae in the legs.

Book lung structure

Much of the published nomenclature related to the structure of the book lung is inconsistent. Purcell (1909) remarked on this inconsistency or confusion more than 100 years ago. Here I will describe each book lung as a series of flattened, roughly horizontal and triangular *air sacs* extending anteriorly from a posterior air sac or *atrium*, and separated by a parallel series of flattened *hemolymph channels* that allow hemolymph to flow between the air sacs, from a ventromedial sinus to a lateral sinus (Figures 2-8, 9.1-9.14; see also Purcell 1909; Snodgrass 1952; Levi 1967; Moore 1976; Hill 1977b, 2006a, 2008b; Anderson & Prestwich 1980; Reisinger et al. 1990; Schmitz & Perry 2000; Brunelli et al. 2015). On each side a lateral (or *pulmo-pericardial*) sinus, covered by thick cuticle (the *operculum* or *cover*), is continuous with, and conveys hemolymph to, a large dorsal sinus, the *pericardium*, surrounding the median, tubular heart of the spider. Note that the term *hemolymph* is used here instead of *blood*, as the arterial system that leads from the spider heart is open-ended, and there is no separation of blood from lymphatic fluid in arthropods. The collecting sinuses that bring hemolymph to the book lungs, and then on to the heart, are not part of this arterial system (Wirkner & Huckstorf 2013).

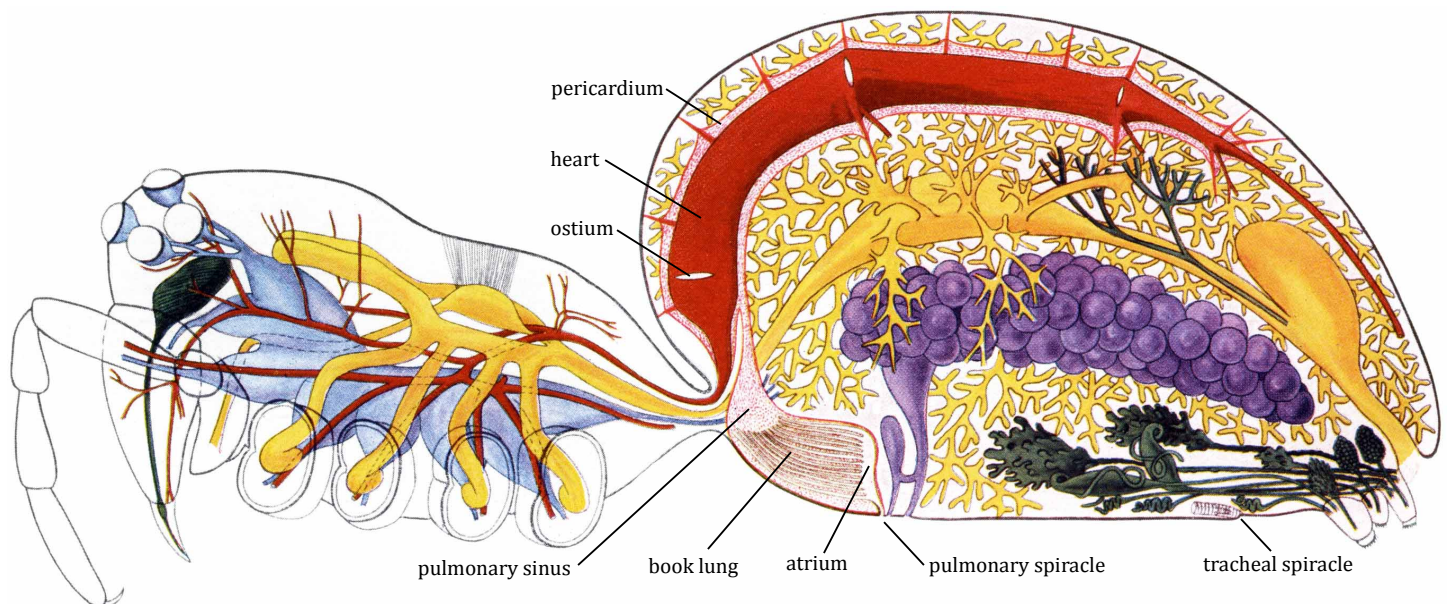


Figure 2. Parasagittal diagram of the major organ systems of a spider, based on a drawing by Comstock (1912), showing the relationship of each book lung to the pericardium and heart. In salticids the tracheal spiracle is further to the rear than shown here, just in front of the anterior lateral spinnerets. The extensive system of tracheae in the opisthosoma, extending medially to the top of the central nervous system in the prosoma, is not shown in this drawing.

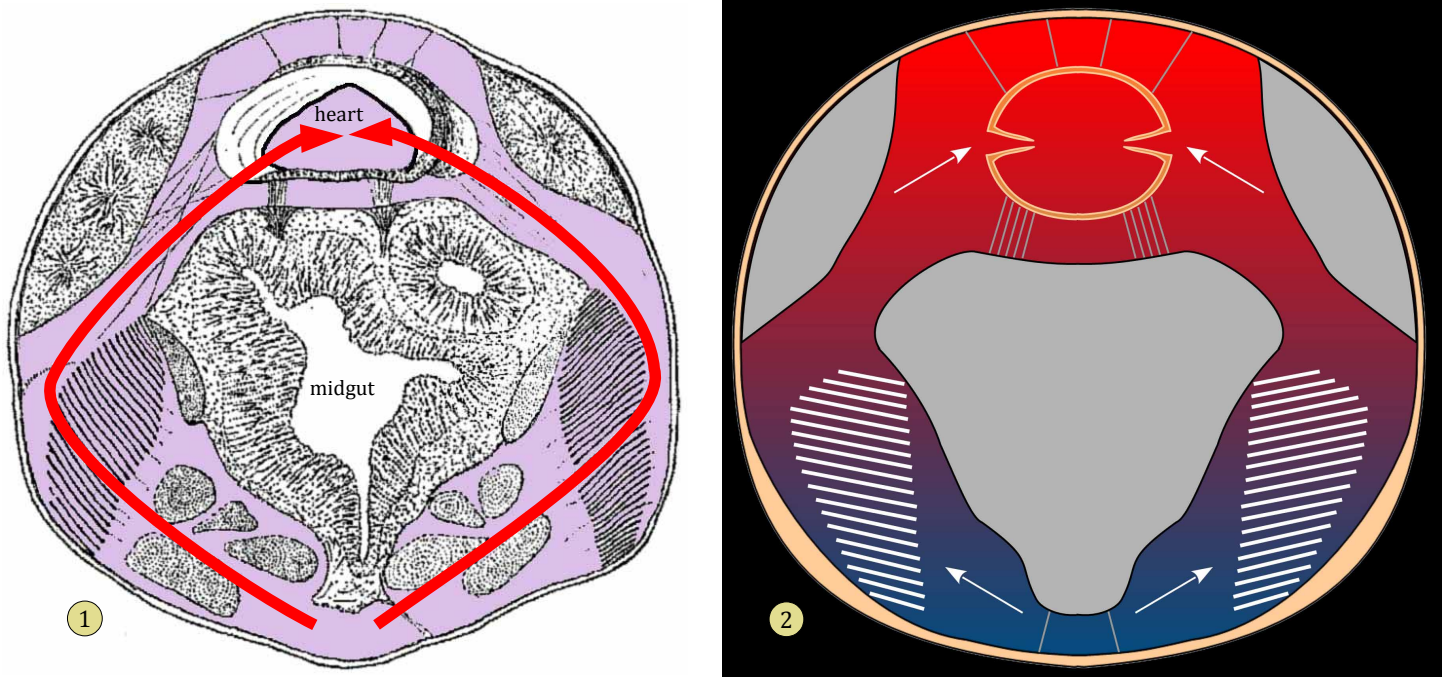


Figure 3. Transverse sections through segment VIII (opisthosomal segment II) of spiders, showing the direction of hemolymph flow from medial (medioventral) sinuses through the air pockets of each book lung to the lateral (pulmo-pericardial) sinuses leading to the pericardium and heart. **1**, Diagram based on a section of *Pholcus* drawn by Willem (1918). **2**, Schematic diagram, colored to indicate the oxygenation of hemolymph as it passes through the book lungs. The color here is only schematic, as spider hemolymph, including circulating hemocyanins and hemocytes, is essentially transparent. Simple one-way valves (ostia) only permit flow in one direction, from the pericardium into the heart, during *diastole*. When the heart contracts (*systole*) they close. In the pericardial cavity, the heart is suspended by many ligaments.

Here I use the term *lamella (membrane)* to refer to the very thin layers of cuticle and attached epithelium (on the hemolymph side) that surround each flattened air sac, separating each air space from the adjacent hemolymph channels on either side (Figures 4, 6). Gas diffusion between each air sac and adjacent hemolymph channel takes place across this thin lamella (Anderson & Prestwich 1980).

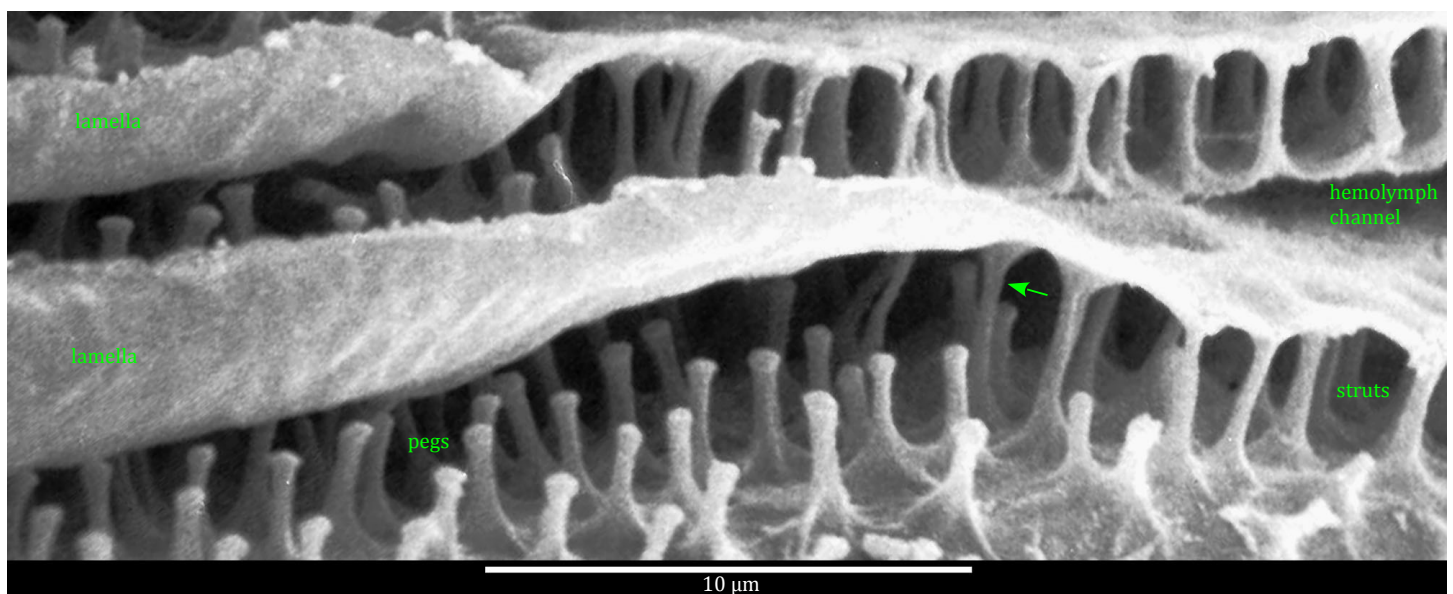


Figure 4. Detailed view of the transition between struts and pegs in the air sacs of an adult male *Phidippus audax* (Hentz 1845). SEM image of cryofractured specimen. Longer struts at the point of transition (arrow) give free play to separation of the unattached lamellar walls of each air sac to the left, permitting expansion of the air space.

Note that other writers have used the term *lamella* either as it is used here (Moore 1976), or to describe the air sacs (Snodgrass 1952; Hill 1977b, 2006a, 2008b; Canals et al. 2007; Brunelli et al. 2015; Farley 2015), the hemolymph channels (Anderson & Prestwich 1980; Foelix 2011), or possibly both (Moore 1976; Küntzel et al. 2019).

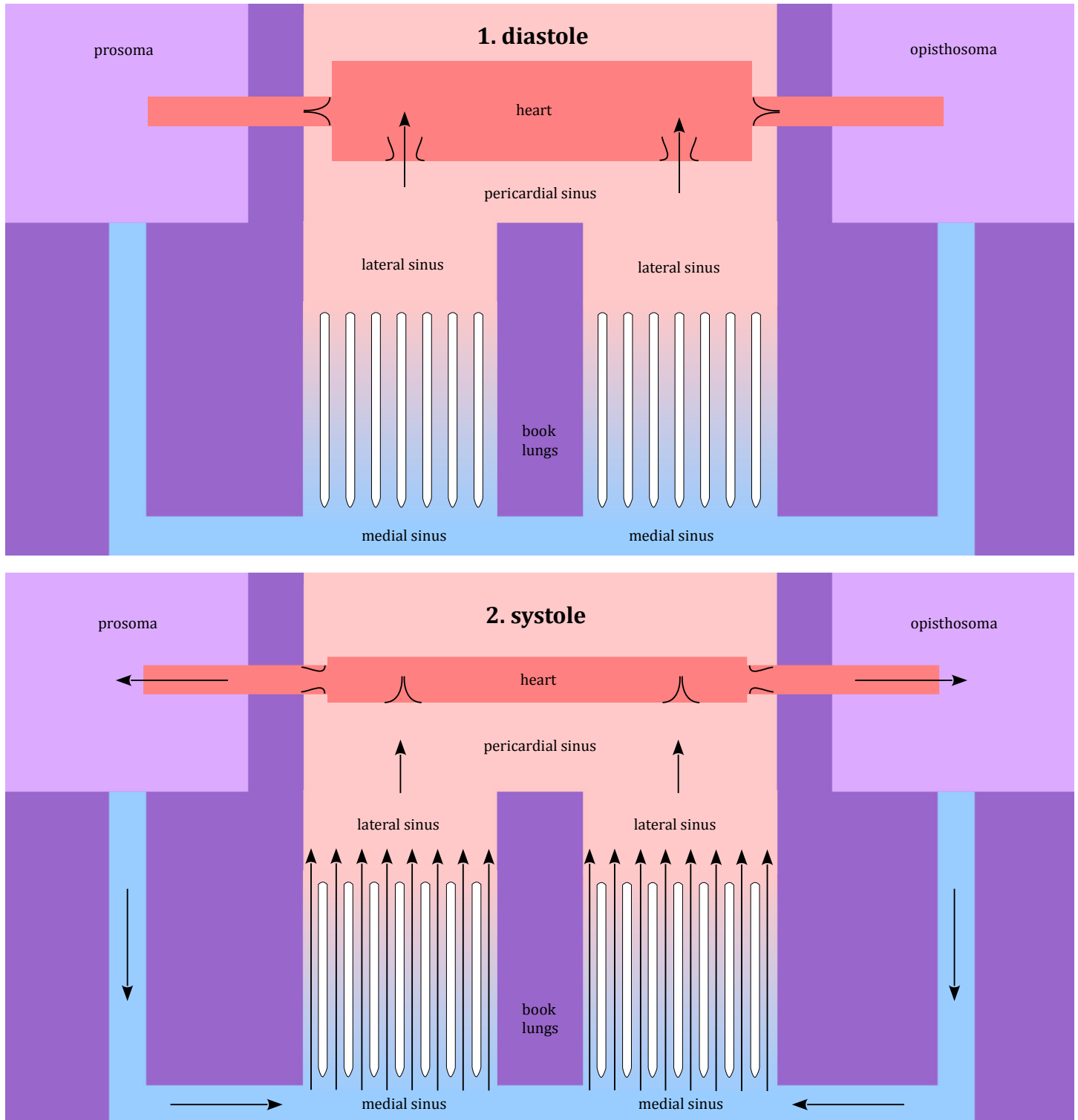


Figure 5. Schematic diagrams showing movement of hemolymph into the heart during diastole (1), and more extensive movement of hemolymph in response to contraction of the heart, or systole (2). Heart contraction produces positive pressure to drive hemolymph through the arteries, and negative pressure (suction) to pull hemolymph through the book lungs.

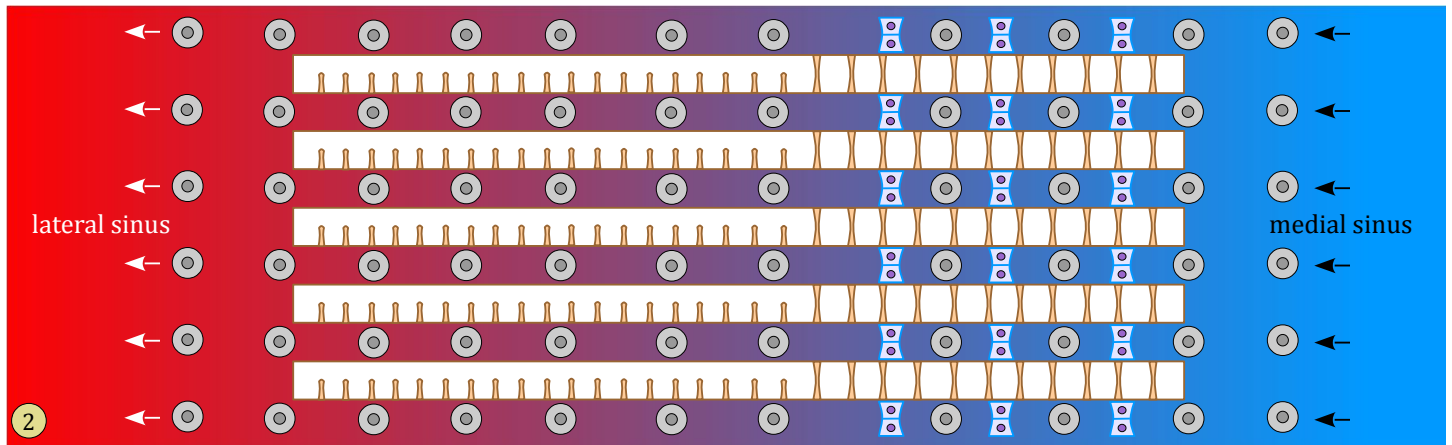
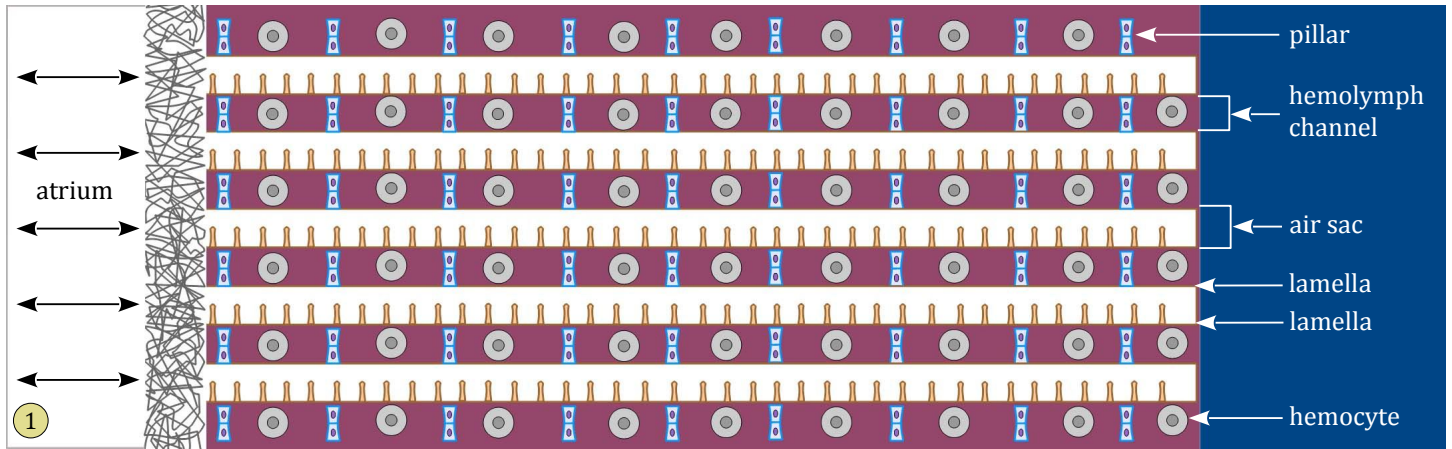


Figure 6. Schematic diagrams showing nomenclature used to describe structure of the book lungs. **1,** Parasagittal view showing anterior (to the right) extension of each flattened air sac into the sinus (divided into flattened hemolymph channels) connecting the medial and lateral sinuses. Pillars comprised of the cell bodies and nuclei of multiple epithelial cells separate adjacent air sacs. Blood cells (circles) can be as wide as the hemolymph channels. **2,** Transverse view showing movement of hemolymph from the medial to the lateral sinus, between the flattened air sacs. Here you can see the separation of the lamellar walls of each air sac by struts (at right), and by pegs (at left).

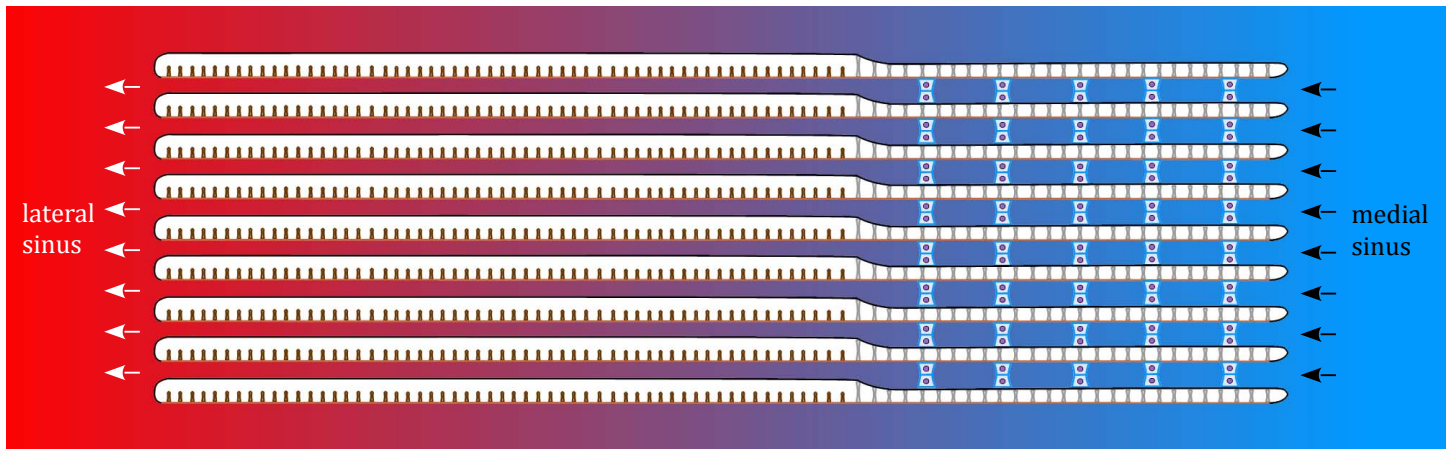


Figure 7. Another schematic transverse view showing the relationship of air sacs to hemolymph channels in the book lung. This drawing is closer to the actual proportions of these structures, which are relatively thin and closely stacked.

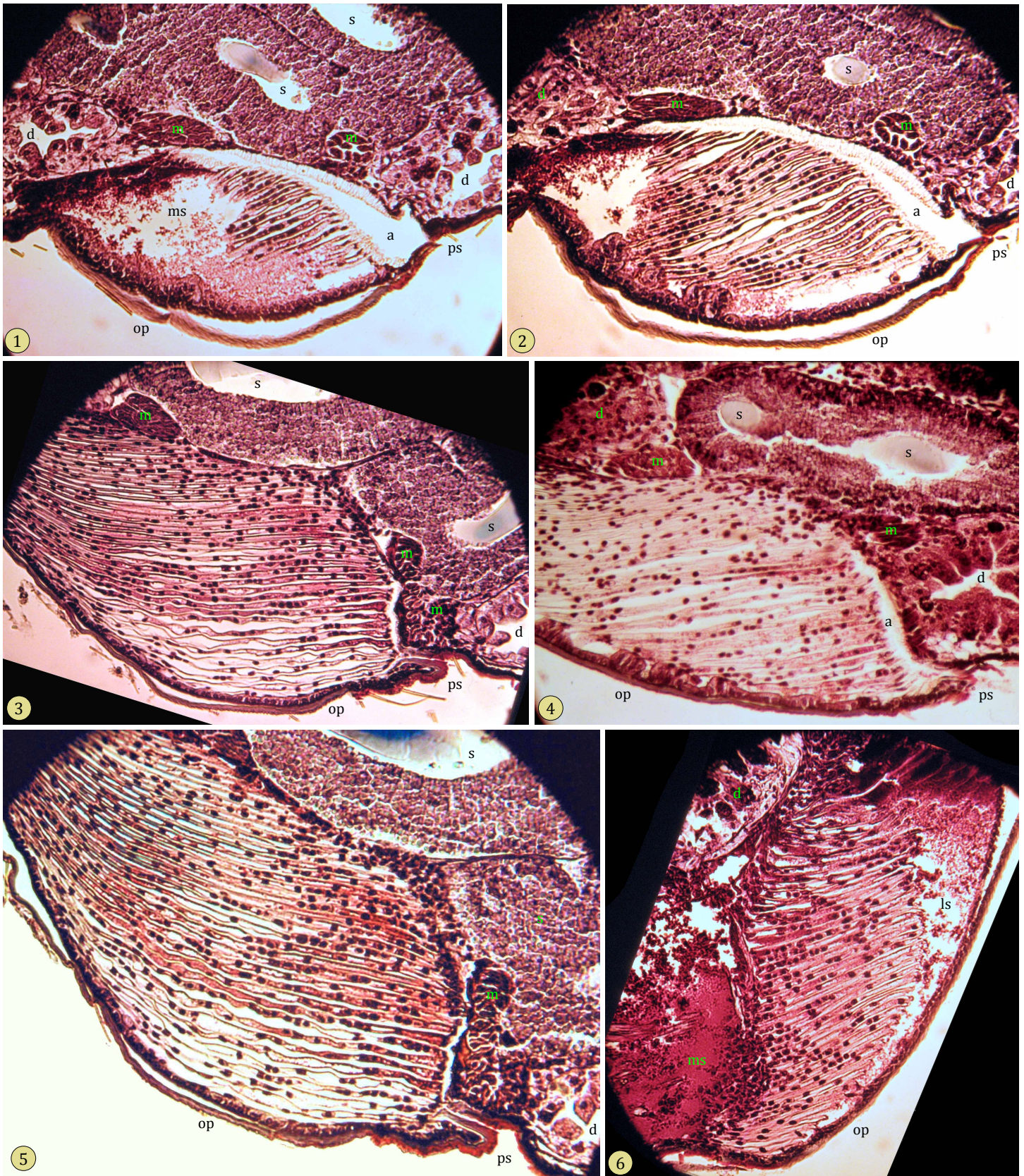


Figure 8 (continued on next page). Serial sections (10 μm) of a female *Phidippus clarus* Keyserling 1885, stained with a modified *Masson Trichrome* stain (Hill 2006b). **1-5**, Parasagittal sections through the book lung. The medial sections (1-2) show the atrium (a), lined with a cuticular mesh on both sides. **6**, Transverse section through a book lung. Other abbreviations: d, digestive gland; ls, lateral sinus; m, muscle; ms, medial sinus; op, operculum (detached by fixation); ps, pulmonary spiracle; s, silk gland.

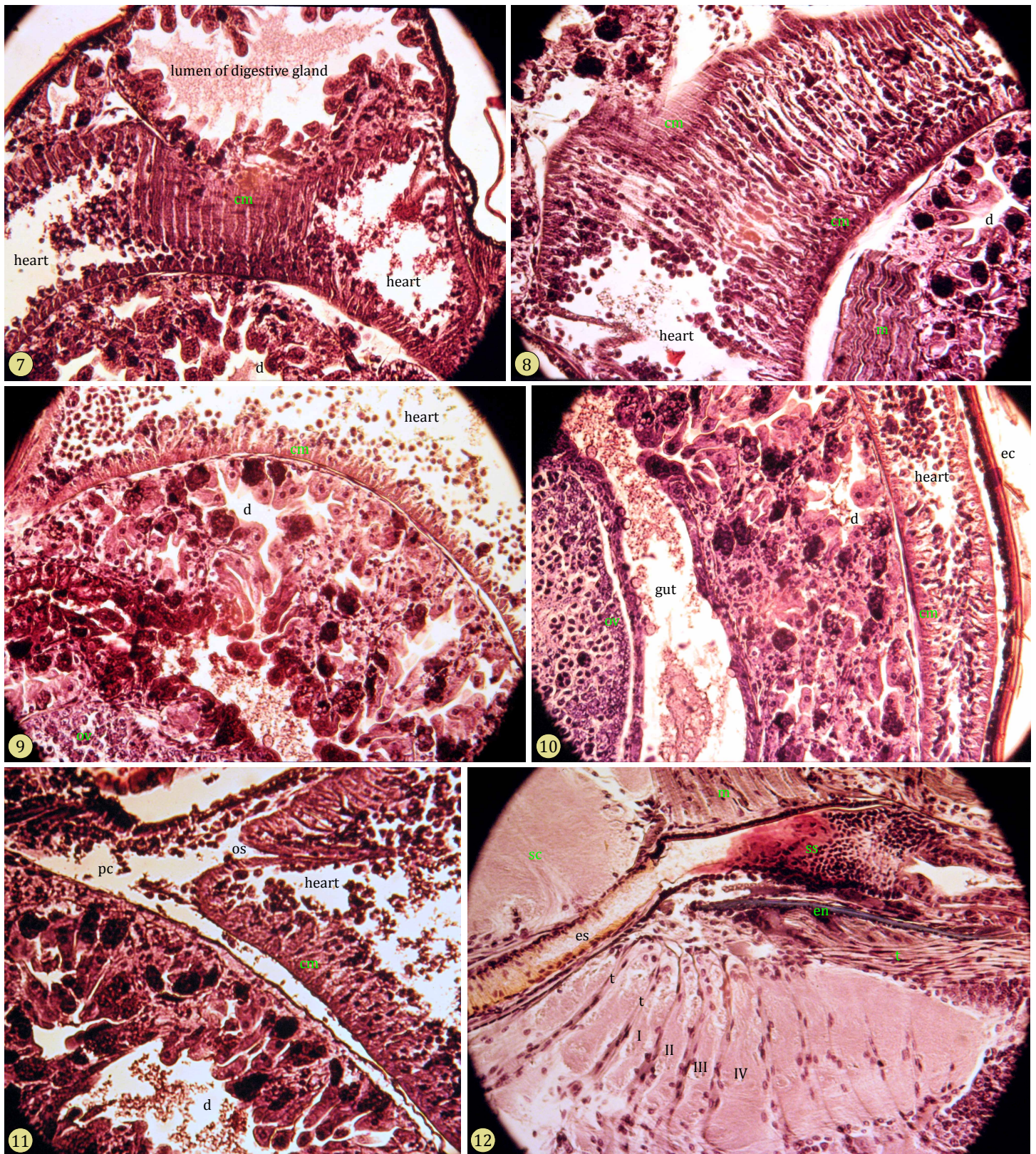


Figure 8 (continued from previous page). Serial sections (10 μ m) of a female *Phidippus clarus* Keyserling 1885, stained with a modified *Masson Trichrome* stain (Hill 2006b). **7-10**, Sections through the heart, showing the position of the heart in the dorsal opisthosoma just above the digestive gland (d), and below the dorsal body wall (10, ec, epidermis with cuticle). **11**, Section through an ostium (os) showing the simple valve that separates the pericardial cavity (pc) from the lumen of the heart. **12**, Sagittal section of prosoma, showing arteries that separate the commissures (I-IV corresponding to leg I-IV ganglia) of the subesophageal ganglion, and the many tracheae (t) beneath the endosternite (en) that serve the fused ganglia of the central nervous system. Other abbreviations: cm, cardiac muscle; es, esophagus; ov, ovary; sc, syncerebrum; ss, sucking stomach.

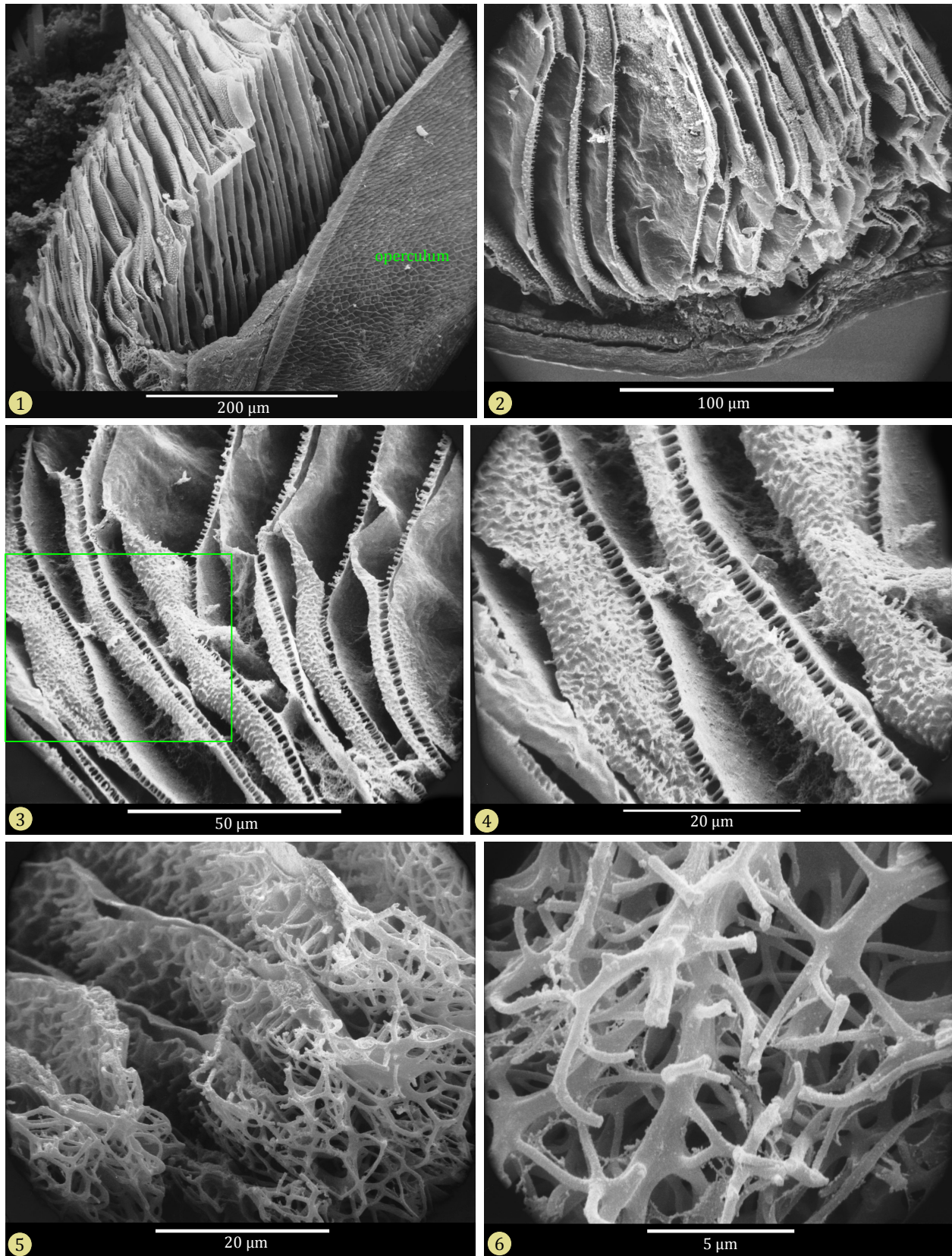


Figure 9 (continued on next page). SEM images of the cryofractured opisthosoma of an adult male *Phidippus audax*. **1-2**, Stacked air sacs of a book lung separated from the operculum by the lateral sinus, transversely fractured. **3**, View of book lung showing both fixed-volume air sacs with struts (bottom), and greatly expanded air sacs with pegs on one lamella (top). **4**, Detail of fixed-volume air sacs with struts, corresponding to the inset in (3). **5-6**, Views of the cuticular mesh that lines the atrium. Note the pegged lamellae and expanded air sacs extending forward from the anterior wall of the atrium (5, upper left).

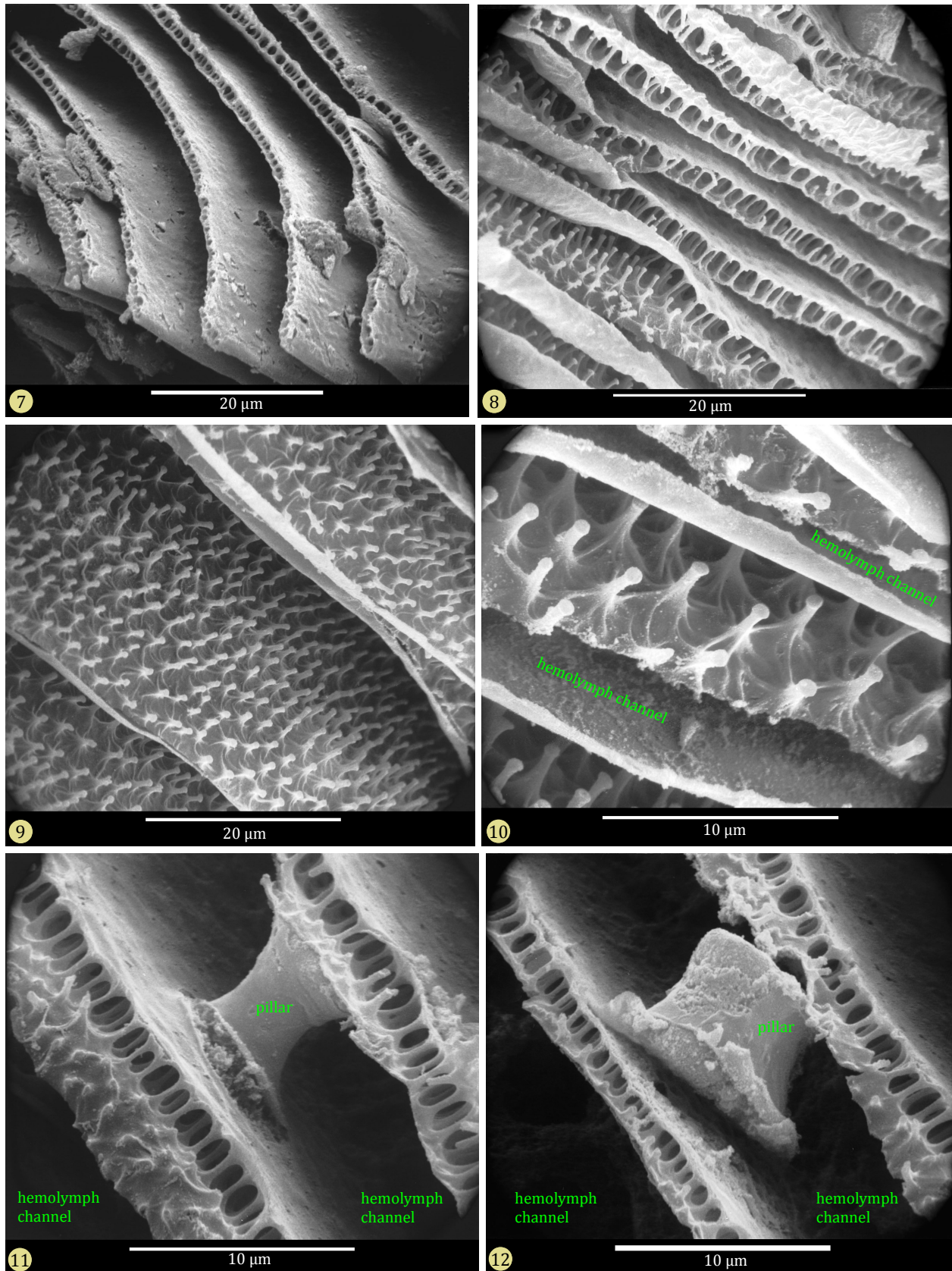


Figure 9 (continued from previous page, continued on next page). SEM images of the cryofractured opisthosoma of an adult male *Phidippus audax*. **7-12**, Book lung. **7**, Thin air sacs with fixed air space separated by wide hemolymph channels near a medial sinus (at bottom). **8**, Transition from struts to pegs (see Figure 4 for detail). **9**, Wide, pegged air sacs. **10**, Detail of pegs showing smooth, rounded apices and buttressing. **11-12**, Two partly dislodged pillars separating narrower air sacs with struts.

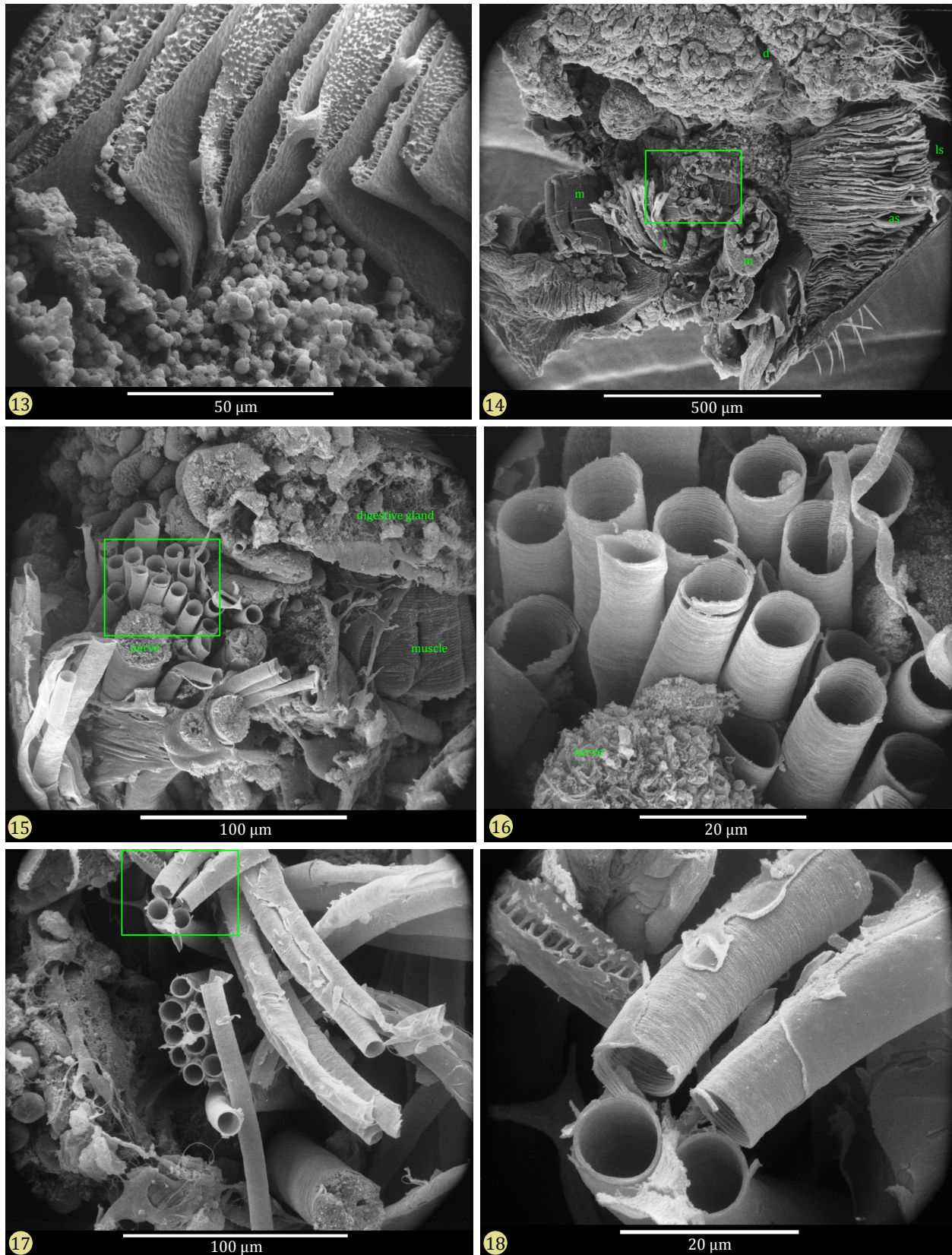


Figure 9 (continued from previous page). SEM images of the cryofractured opisthosoma of an adult male *Phidippus audax*. **13**, Hemocytes in a medial sinus (at bottom) and air sacs with struts separated by wide hemolymph channels (top). **14**, Transverse fracture of anterior opisthosoma through book lung. **15**, Inset (14) showing bundles of tracheae and associated nerves that pass through the pedicel to the prosoma. **16**, Inset (15). **17**, More tracheae near nerves. **18**, Detail from inset (17) showing cytoplasm around the tracheae, and nearby pulmonary air sac. Abbreviations: as, pulmonary air sac; ls, lateral sinus; m, muscle; t, tracheae.

It appears that the spiracle that can be opened to let air into each atrium is usually closed in salticids, so gas exchange through the spiracle is discontinuous. Each atrium is lined anteriorly and posteriorly with a *cuticular mesh* of irregular struts through which air can pass (Hill 1977b, 2006a, 2008b; Brunelli et al. 2015). This mesh ensures that at least a minimum volume of air is maintained in the atrium at all times, and may also act as a filter to prevent the entry of foreign material into the flattened air sacs. Robinson & Paim (1969) described the presence of spiracle dilator muscles that could expand the atrium by pulling the posterior atrial wall to the rear, but they did not find any muscles to oppose this movement, in *Araneus*. They thought that this could be accomplished by *elastic rebound* of the spiracle after relaxation of the dilators, much like the spiracular mechanism later described for the scorpion *Paruroctonus* by Farley (1990). Snodgrass (1952) also reported that only spiracle dilators were present. However, longitudinal compressor muscles that connect to the body wall and endosternites may also provide this opposing force by pulling the anterior opisthosoma, to the front of the epigastric furrow, together with the posterior opisthosoma.

Collapse of the flattened air sacs is prevented by either fixed cuticular *struts* that join both dorsal and ventral lamellae (walls) of each air sac, or by *pegs* that are attached to only one of these lamellae, permitting expansion of the contained air space (Moore 1976; Hill 1977b, 2006a, 2008b; Anderson & Prestwich 1980). These develop from epithelial cells that occupy that air space during development (Farley 2008). Struts are generally found toward the medial edge of each air sac, where blood enters from the medial sinus, and pegs are generally found toward the posterior edge of each air sac, where air is exchanged with the atrium, or toward the lateral edge of each air sac, where hemolymph leaves the channels of the book lung to collect in the lateral or, pulmo-pericardial sinus. Here I use the terms *strut* and *peg* to describe the structures that support the air space, but it should be noted that these have been given a variety of names by other writers, to include *blunted spines* (Purcell 1909) and *cuticular trabeculae* (Brunelli et al. 2015).

Hemolymph channels through the book lung are kept open by *pillars*, each comprised of the cell bodies including nuclei of 2-4 *pillar cells*, the cytoplasm of which extends in a very thin layer as part of the surrounding lamellae, thus separating the hemolymph channel from the cuticle of each air sac (Reisinger et al. 1990; Schmitz & Perry 2000; Brunelli et al. 2015). Pillar cells are joined at these pillars by desmosomes and gap junctions, and their intracellular skeleton of microtubules provides them with the rigidity required to prevent collapse of the hemolymph channels (Brunelli et al. 2015). Each pillar is wider in the direction of hemolymph flow, and narrower in a direction perpendicular to this, apparently lowering the resistance of each channel to the flow of hemolymph. The extent to which these pillars are elastic and can thus contribute to dynamic expansion of the hemolymph channels is not known, but they may have little or no presence in the lateral part of those channels, where the air sacs are capable of expansion.

Diffusion and the question of book lung ventilation

Because of their apparent sufficiency with respect to surface area available for gas exchange, spider book lungs and tracheae have been thought to operate exclusively through the diffusion of gas molecules between the atmosphere and various tissues, with virtually no ventilation of the intervening air spaces in the atrium and the flattened air sacs of each book lung (Paul et al. 1987; Schmitz & Perry 2000, 2001). Related calculations have not taken the impact of tortuosity (interrupted pathways) on diffusion through these air spaces into account. However several observations suggest that some ventilation does occur in the air sacs of the book lung.

First, direct observation of the heart, book lungs, and associated sinuses of a number of spiders, to include the salticid *Lyssomane viridis* (Walckenaer 1837) and the pholcid *Pholcus phalangioides* (Fuesslin 1775), has revealed movement of at least the lateral edge of air sacs, and blood in the lateral sinus, as well as deformation of the overlying cuticle, all in synchrony with cardiac systole (Willem 1918; Hill 1977b, 2006a, 2008b). Moore (1976) also suggested that "the lamellae seem to possess some peristaltic movement - the surface undulates gently in a pumping action." Earlier, Snodgrass (1952) reported that pulsating hemolymph might play a role in book lung ventilation. In his observations of *Pholcus*, Willem (1918) described the role of epicardial ligaments in transmitting oscillations in synchrony with cardiac systole (130 cycles/minute). Above the book lungs he observed a synchronous rise of the dorsomedial cuticle in association with distension of the anterior aorta, accompanied by a sagging of the pulmo-pericardial sinuses, related to a reduction in hemolymph pressure. He also determined that, also in synchrony with each depression of the pericardial cavity, the operculum over each book lung was pulled in slightly (by $\sim 10 \mu\text{m}$) by this apparent reduction in pressure, as the system of lamellae [air sacs] of the book lung saw a decrease in compression that could be compared to the expansion of an accordion.

I have observed the same synchronous up-and-down movement of the flattened air sacs through the semi-transparent cuticle of the salticid *Lyssomanes viridis*, corresponding to a heart rate of 150-210 cycles/minute (Hill 1977b, 2006a, 2008b). This movement was most evident for the most dorsal air sacs, corresponding to the decline in fluid pressure in the lateral or pulmo-pericardial sinus that accompanies cardiac systole (*fluid pressure pump* or *suction pump*; Stewart & Martin 1974; Paul et al. 1989, 1994; Paul & Bihlmayer 1995; Wirkner & Huckstorf 2013). This could power expansion of the air spaces that were separated only by pegs, and not fixed by struts, according to a *hemolymph bellows hypothesis* for lung ventilation, later called the *bellows hypothesis* (Foelix 2011). Schematic drawings that depict alternative ways that the air sacs might move in synchrony with the heart beat are shown in Figure 10.

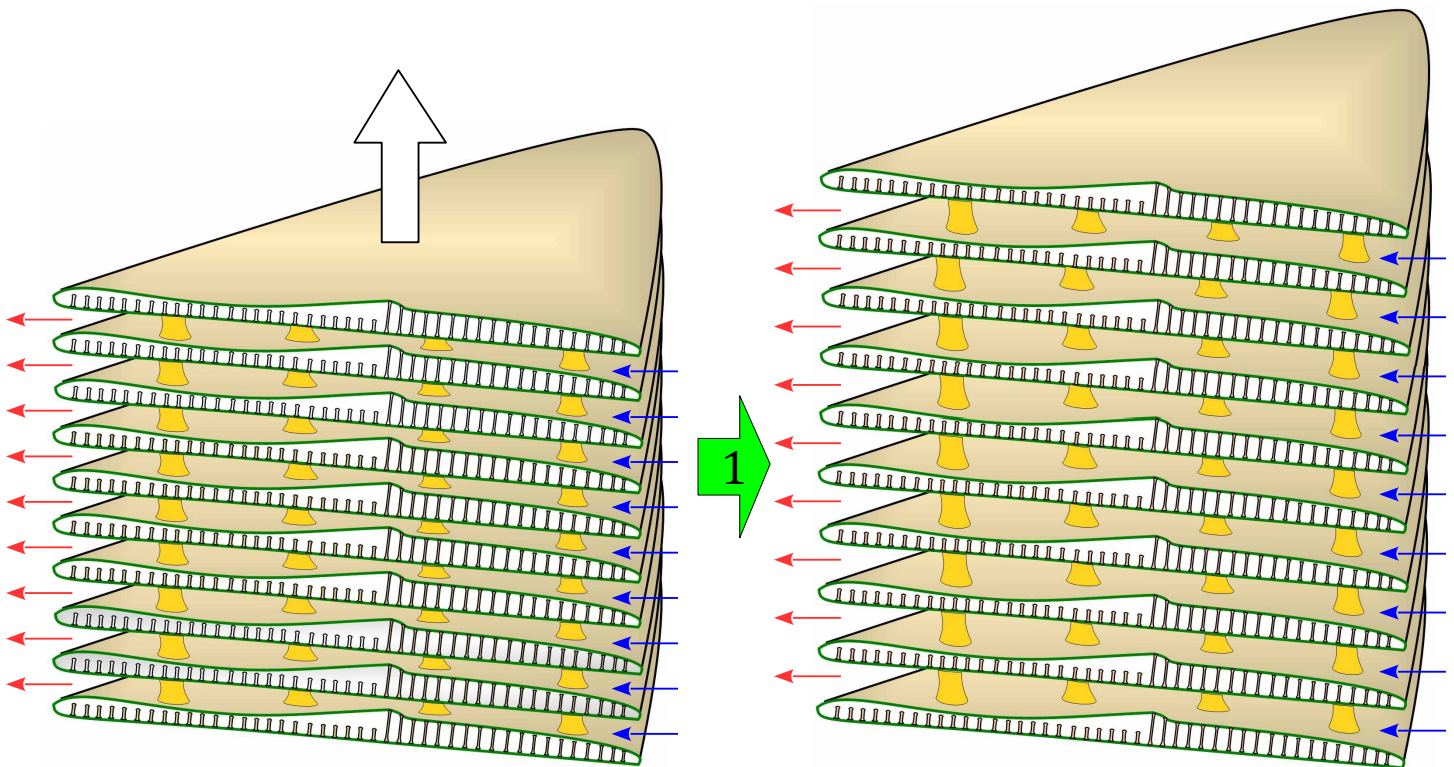


Figure 10.1. Simple accordion-like expansion of the stack of air sacs, or at least the upper set of air sacs, might explain the observed up-and-down movement of these sacs in lateral view. As shown here, this might not involve significant expansion of the air spaces, but it would require elasticity of the pillars. In this model the air spaces and hemolymph channels could still oscillate, mixing air even in the absence of tidal ventilation.

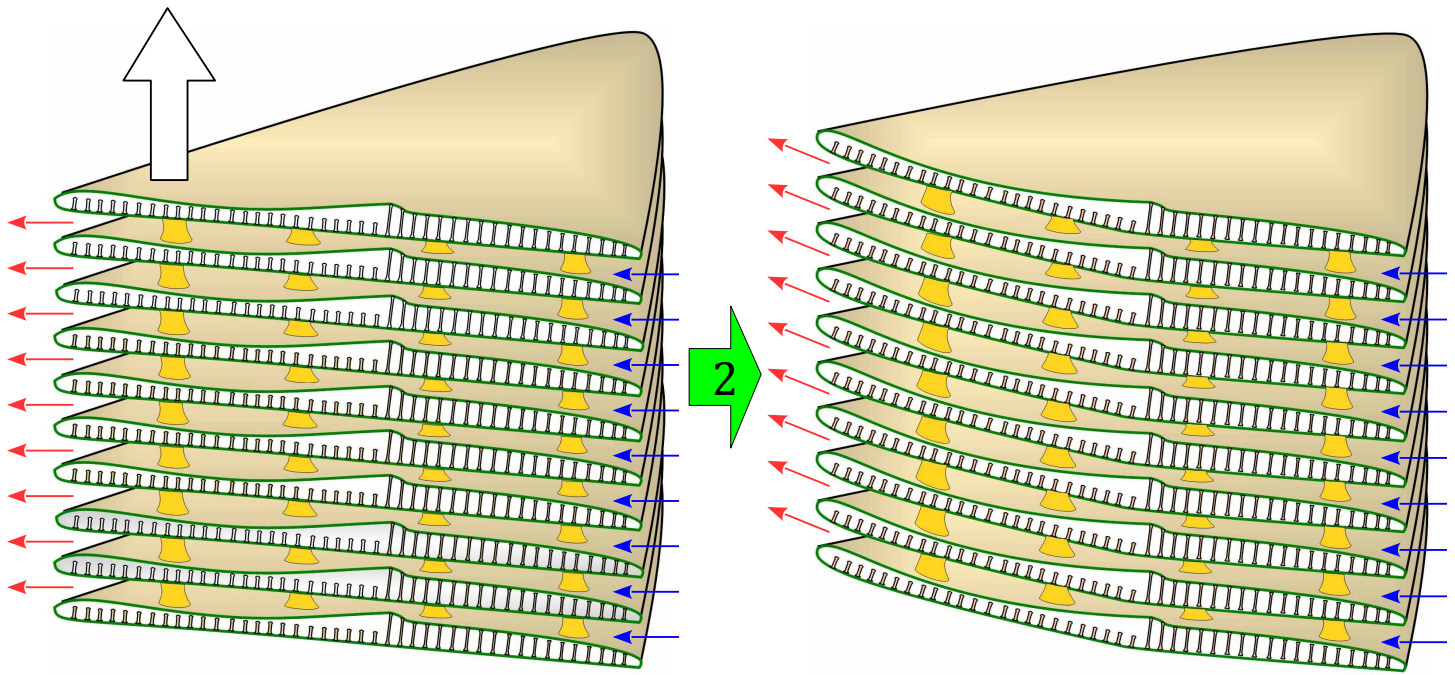


Figure 10.2. Up-and-down oscillation of the more flexible lateral parts of the air sacs without significant expansion. Like (10.1), this model accounts for the observed movement of the air sacs, but it does not require significant elasticity of the pillars. Mixing as a result of rapid oscillation could still take place.

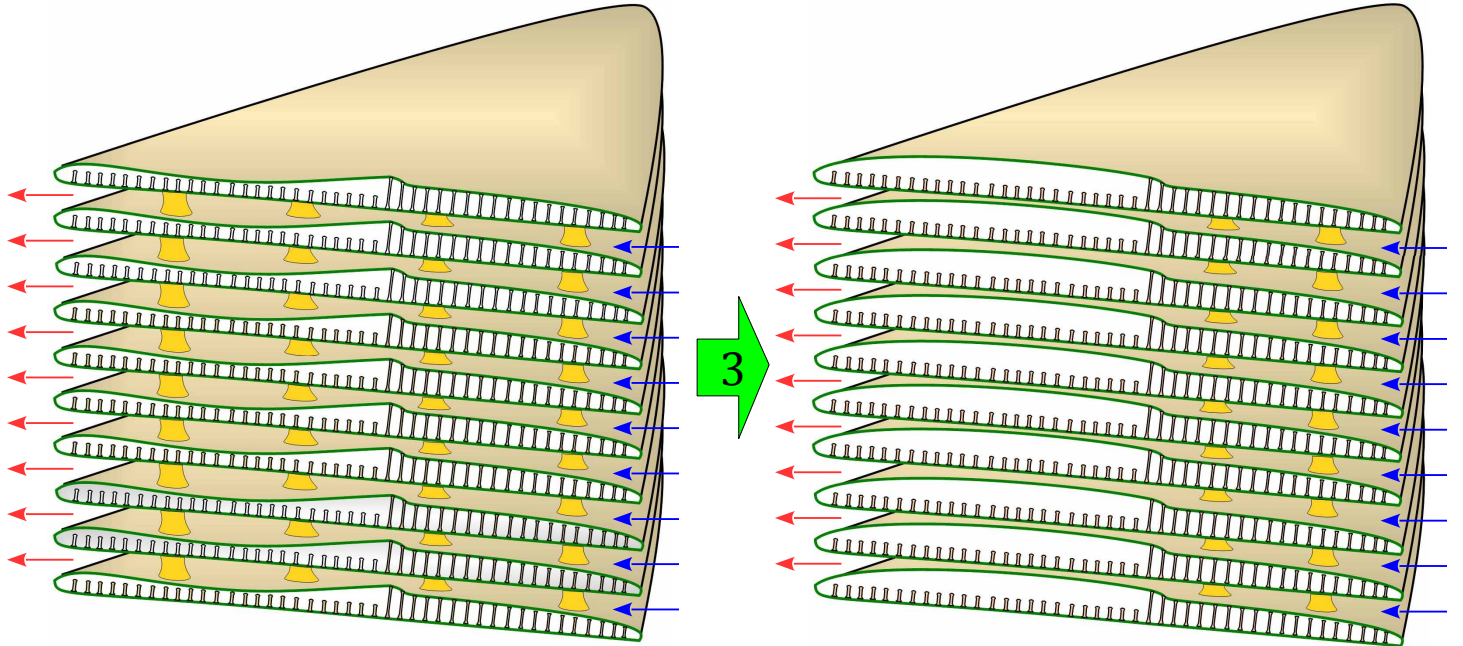


Figure 10.3. Expansion of the pegged, flexible portion of the air sacs with limited vertical movement of each sac. This model corresponds to earlier diagrams of the hypothetical *hemolymph bellows* (Hill 1977b, 2006a, 2008b; Foelix 2011), but does not account for the observed up-and-down movement of the lateral margin of each sac.

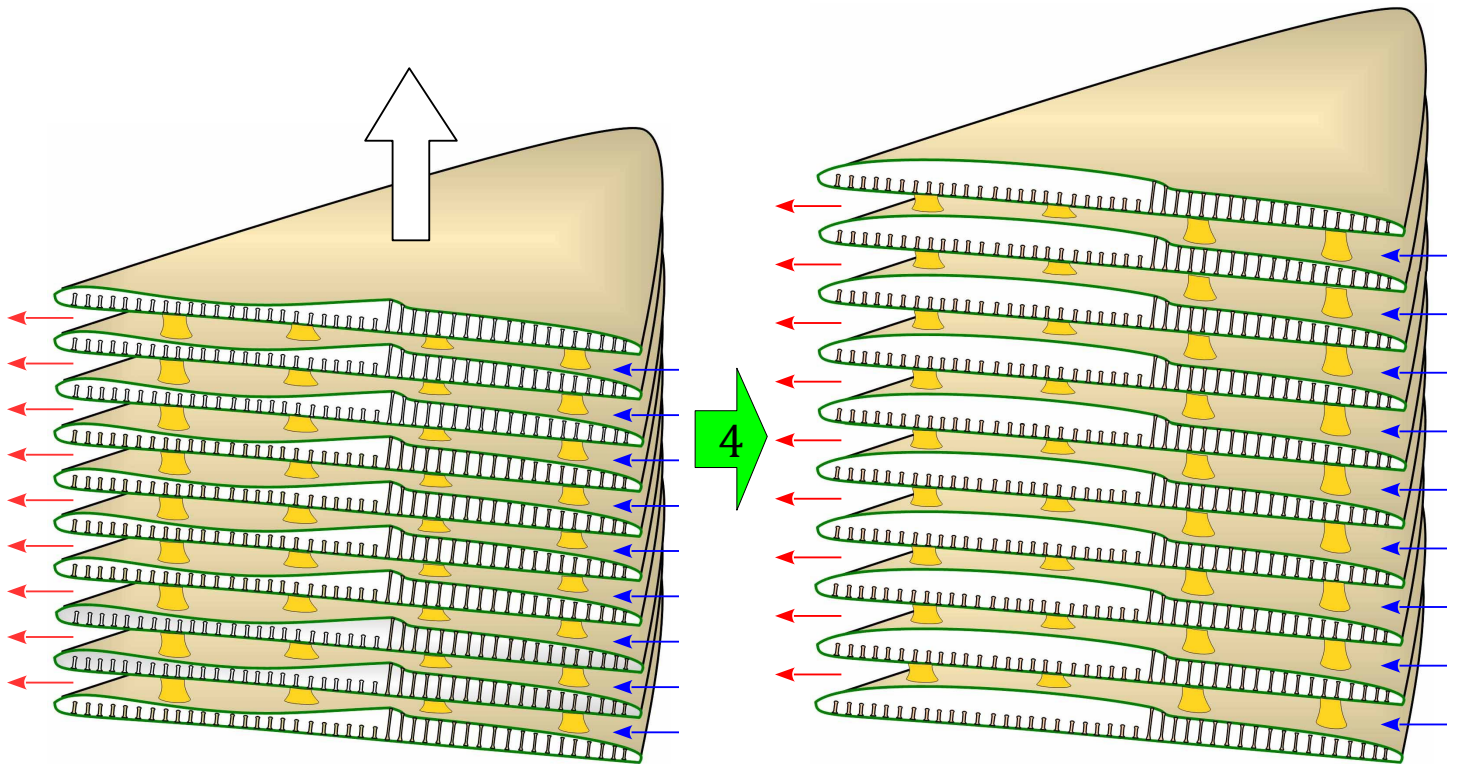


Figure 10.4. Expansion of the pegged, flexible portion of the air sacs in association with accordion-like expansion of the stack. Like (10.1), this model requires elastic pillars.

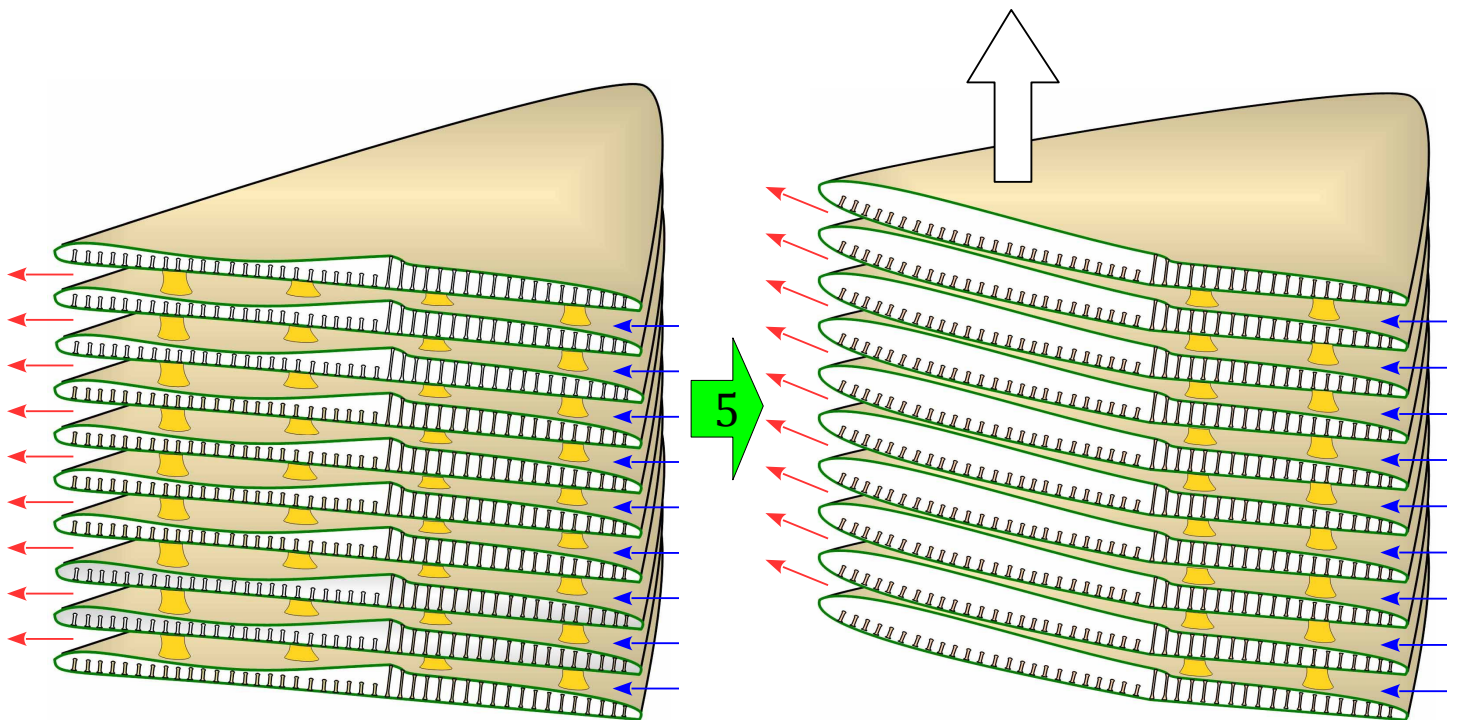


Figure 10.5. Expansion with up-and-down movement of the pegged, flexible portion of the air sacs. This allows for less elastic pillars between the fixed, medial air spaces. I have not found images showing pillars between the pegged parts of the air sacs, but if these were present (as shown at left) they could undergo some compression.

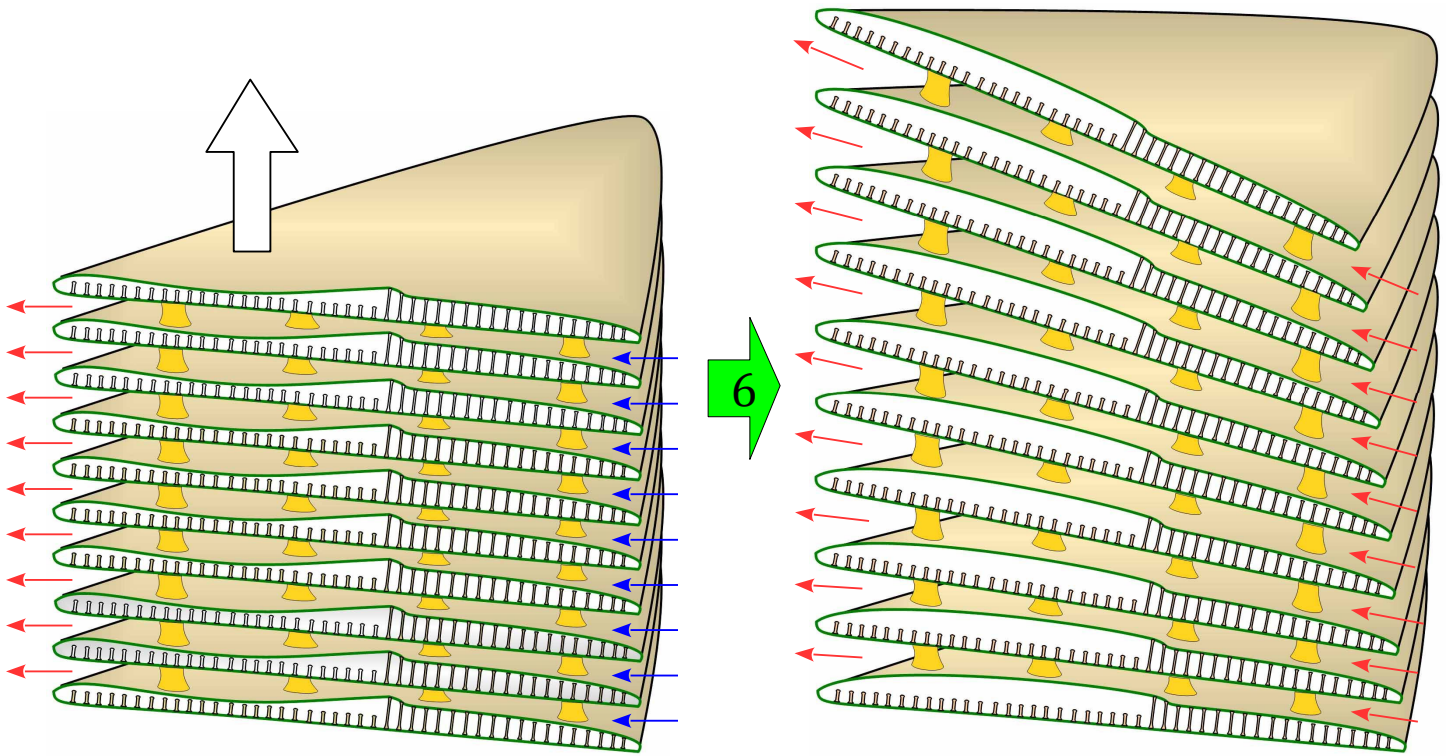


Figure 10.6. Accordion-like expansion of the pegged, flexible portion of the air sacs in association with variable rotation of the entire stack. This requires elastic pillars, but this diagram also exaggerates the extent of movement that would actually take place, and the width of the flexible air spaces might oscillate with undulation of their thin, flexible lamellae. Based on the fact that the lamellae are very thin, this oscillation almost certainly takes place, with undulation of the unpegged lamella, in any of the models shown here (10.1-10.6).

Hemolymph can transmit pressure waves or oscillations, but it is also largely incompressible. However the opisthosoma is flexible and this could accommodate local changes in fluid volume, as recognized by Willem (1918) in his observations of movement of the body wall of the middorsal and anterior opisthosoma. We do not know the extent to which the opening and closing of each pulmonary spiracle, the compression of air in the atrium as each spiracle is closed, and changes in both PO_2 and PCO_2 affect the volume of the pulmonary air sacs. These are factors to consider in future studies with advanced imaging technology to allow more detailed observation of living animals.

Anderson & Prestwich (1980) suggested that, in addition to the anatomical evidence for the expansion of air sacs, the scaled dimensions of spider book lungs supports the hypothesis that active ventilation is important. Since Paul & Bihlmayer (1995) found that the heart rate of a spider can increase by a factor of 10 during activity, and the stroke volume associated with systole can also vary, future studies of the movement of book lungs and associated structures should include spiders with varying heart rate.

An alternative hypothesis for the movement of the air sacs of the book lungs is based on their movement by hypocardial ligaments, known to move other structures of the anterior opisthosoma in synchrony with the heartbeat (Willem 1918; Weiss 1923; Snodgrass 1952). This may represent the principal cause of air sac movement, or it may contribute to a synchronous pulmo-pericardial suction effect, to either move or to inflate the air sacs. In a more recent study of the scorpion *Paruroctonus*, Farley (1990) similarly described the role of hypocardial ligaments extending from the heart to the book lungs as the cause of their dorso-ventral movement or oscillation in response to heart beat, and suggested that this movement could increase ventilation or gas exchange through the air sacs.

As discussed previously, in addition to oxygen supply, both oxygen toxicity and water loss are major considerations for terrestrial animals. Although in theory diffusion alone could account for the oxygen supply needed by small insects, recent imaging technology has revealed that ventilation or convection of air contained in the air sacs or tracheae is still the norm for these animals (Socha et al. 2010). Active ventilation in insects has generally been associated with compression of the tracheae or air sacs (Westneat et al. 2003; Socha et al. 2008). In the grasshopper *Schistocerca*, sophisticated imaging has also revealed synchronization of air sac or tracheal trunk compression with the heartbeat (Lee & Socha 2009).

Insect spiracles are not always open, and several observations suggest that the spiracles of spiders are closed most of the time (e.g., Willem 1918; personal observations). The *discontinuous gas exchange cycle* (DGE or DGC) has been studied in many insects that open and close their spiracles. This is associated with a burst of CO₂ release each time that spiracles are opened (Contreras & Bradley 2009). The DGC includes three stages: a *closed* stage, in which O₂ in the air spaces is depleted as CO₂ accumulates, an unsustainable *flutter* stage in which the spiracles open intermittently and partially to maintain a minimal level of O₂ in the air spaces as CO₂ continues to accumulate, and an *open* stage in which O₂ moves rapidly into the air spaces as the accumulated CO₂ is released (Quinlan & Gibbs 2006; Lighton 2007; Boardman et al. 2011). Related to these cycles is the fact that, when compared to O₂ obtained from the atmosphere, diffusion of CO₂ is a relatively slow process (Woods 2011). Several hypotheses, all unresolved, have been advanced and then critically challenged as explanations for the existence of DGC in insects. These include (1) energy-saving *metabolic downregulation* with inactivity (Chown 2011), (2) *water retention* (the *hygric hypothesis*; Sibul et al. 2006; Schimpf et al. 2009; Chown 2011; Woods 2011), (3) *prevention of oxygen toxicity* (oxidative damage), or *oxygen regulation* (Hetz & Bradley 2005; Lighton & Ottesen 2005; Lighton & Turner 2008; Contreras & Bradley 2009; Boardman et al. 2011), (4) oxygen regulation in normal and hypoxic environments (*chthonic hypothesis*; Woods 2011), and (5) *defense* to prevent invasion of the air spaces by parasites (Woods 2011). Solifugids, otherwise acyclic, also use DGC (discontinuous emission of CO₂) when they are inactive or subject to arid conditions (Sláma 1995). This behavior is in agreement with both (1) the *metabolic downregulation* and (2) the *hygric* hypotheses. In insects that switch between DGC and CGE (continuous or acyclic gas exchange), DGC has been shown to reduce water loss but not metabolic rate (Williams et al. 2010).

As part of *oxygen regulation*, it has been suggested that the presence of *reactive oxygen species* (ROS) or potentially damaging oxidative agents in the hemolymph or tissues of insects may determine the timing of DGC in insects, a view supported by the maintenance of a very low amount of oxygen in the air spaces (PO₂ ~ 2-4 KPa), compared to a much higher level of atmospheric oxygen (PO₂ ~ 50 KPa). Since diffusion across the book lung lamellae of the spider *Grammostola* also involves a very low gradient (Δ PO₂ ~ 0.12-0.16 KPa; Canals et al. 2007, 2015), we can surmise that spiders need to diffuse O₂ across a very low lamellar gradient as O₂ is depleted, and CO₂ accumulates, in the air spaces when the spiracles are closed. This opens up the possibility that, as in small insects, active ventilation, oscillation, or agitation of the air sacs can contribute to reduction of the limit to which the lamellar O₂ gradient can be reduced and still deliver the required level of O₂ to the hemolymph. We can think of the closed air spaces of the book lung as a regulated *rebreather* that allows the slower process of CO₂ accumulation for release to catch up with the otherwise faster process of O₂ uptake.

Tracheal system

The single tracheal spiracle of salticids and other entelegynes is located far to the rear, just anterior to the spinnerets (Figures 9.14-9.18, 11-12).

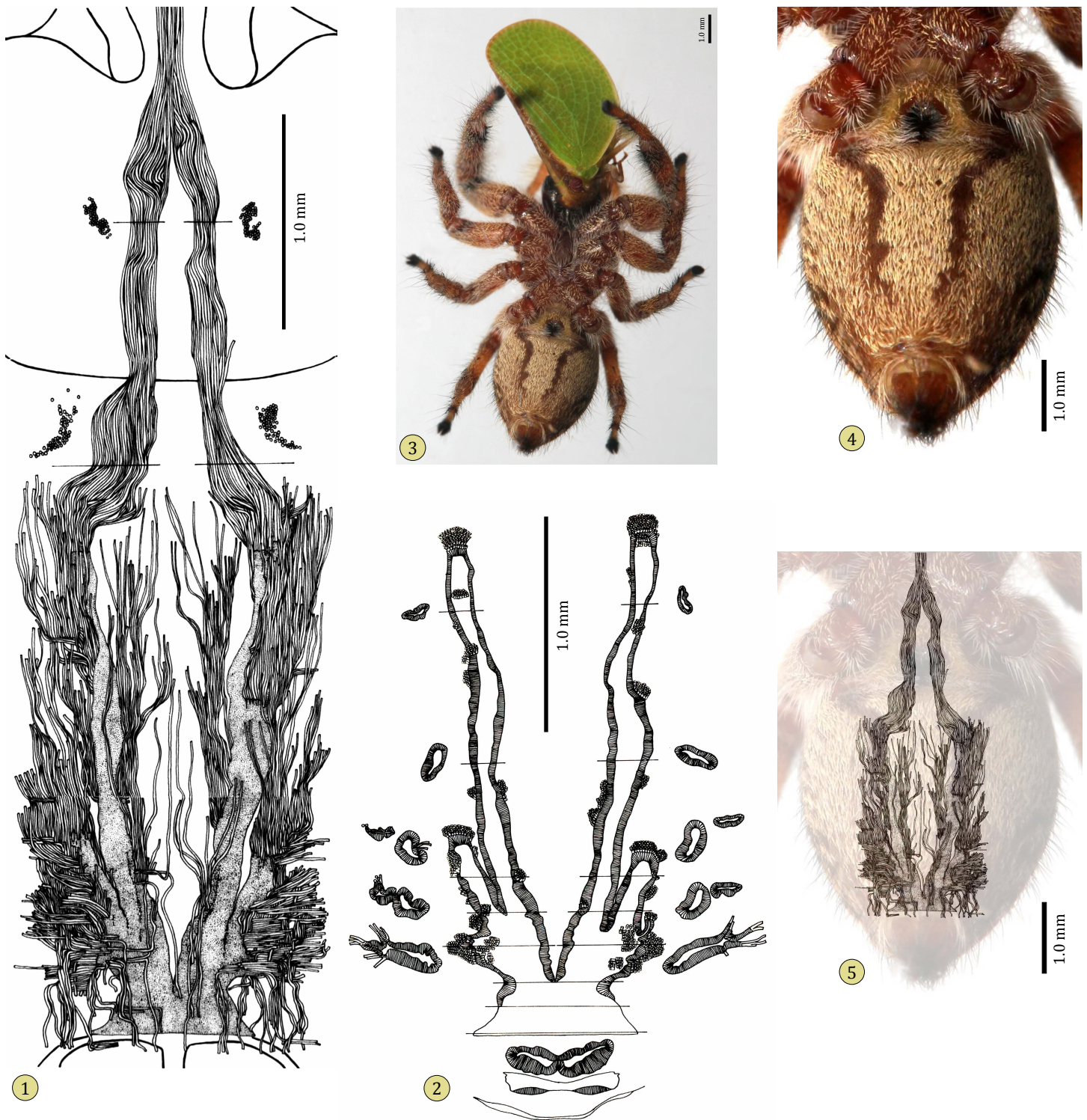


Figure 11. Reconstruction of the tracheal system of an adult female *Phidippus clarus* from serial (10 μ m) transverse sections (after Hill 1977a, 2008a). **1**, Reconstruction of the flattened, branching air sac and connected tracheae from the anterior spinnerets (at bottom) to the pedicel (at top). Not all distal terminations of the tracheae in the opisthosoma are shown. Several transverse sections of tracheal bundles are shown in the anterior opisthosoma, where they merge to form a single bundle that enters the prosoma above the opisthosomal nerves. **2**, Reconstructed horizontal section of the air sac, with terminations of the bundles of tracheae that emerge from this sac. Horizontal lines correspond to the location of the transverse sections that are presented to either side of the main figure. The lack of a cuticular mesh near the wide tracheal spiracle (at bottom) allows this to be closed completely, but we know little of how this is used. **3**, Ventral view of a feeding adult female *Phidippus clarus*. **4**, Detail of ventral opisthosoma, from (3). **5**, Position of the tracheal system in the opisthosoma of *P. clarus*. Compare with (4).

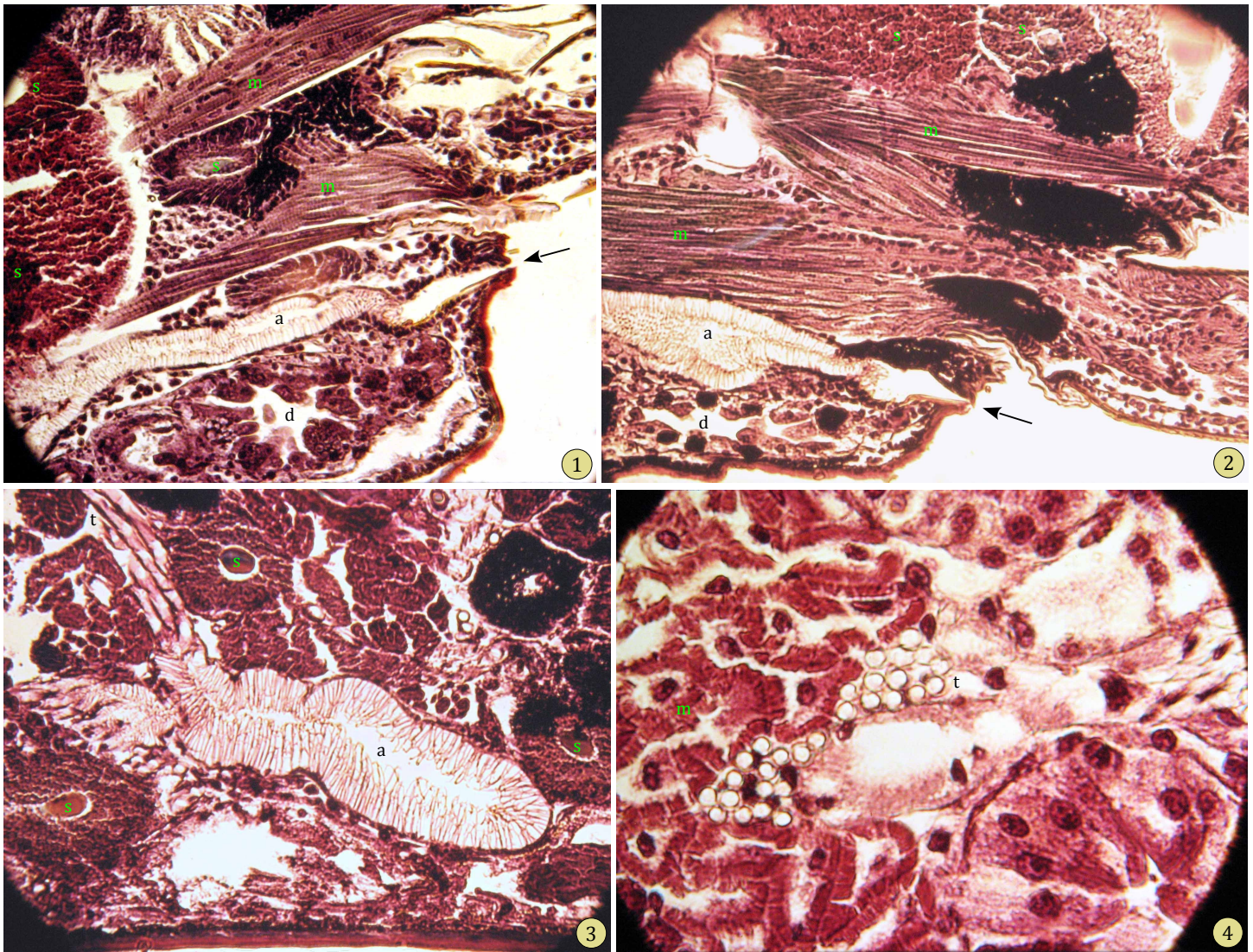


Figure 12. Serial sections (10 μm) of the opisthosoma of a female *Phidippus clarus*, stained with a modified *Masson Trichrome* stain (Hill 2006b). **1-2**, Two parasagittal views of the distal opisthosoma, showing the tracheal spiracle (arrows) and the air sac (a) that extends anteriorly (to the left) from this spiracle. Note the relationship to some of the many muscles of the spinnerets (m), and nearby silk (s) and digestive (d) glands. **3**, Transverse section of one of the main branches of the air sac, corresponding to one of the sections shown in Figure 11.2. Note the surrounding silk glands (s). The ventral wall of the opisthosoma can be seen at the bottom of this image. **4**, Transverse section showing tracheal bundles passing near muscle cells (m). Cells in the lower right of this image appear to be part of the digestive gland that occupies much of the opisthosoma.

The *tracheal spiracle* opens to a ventral, branching *air sac* in the opisthosoma. Like the atrium of each book lung, this air sac is lined with a *cuticular mesh* that prevents its collapse. From this air sac numerous bundles of *tracheae* emerge. Beyond the air sac, the tracheae of salticids do not branch and there is no anastomosis. The fact that the walls of the tracheae, comprised of ringed or coiled endocuticle surrounded by a thin layer of epithelial cytoplasm (Figure 9:14-18), are of uniform thickness, suggesting that diffusion of gases take place along their entire length (Schmitz & Perry 2000).

Schmitz & Perry (2000) used a somewhat different nomenclature, describing an *atrium* or entry chamber in association with the tracheal spiracle, leading to wider, branching *tube tracheae* (my *air sac*), in turn leading to many *secondary tracheae* (my *tracheae*). As shown in Figure 11, these tracheae lead primarily to the digestive gland in the opisthosoma on either side, and through the pedicel to the central nervous system in the prosoma (Figure 8:12).

The tracheal systems of few salticids have been described to date, and all seem to agree in general structure (Lamy 1902, *Ballus*, *Heliophanus*, *Salticus*; Hill 1977a, 2008a, *Phidippus*; Schmitz & Perry 2000, *Euophrys*, *Salticus*). The tracheae of spiders are thought to operate by diffusion with no active ventilation (Paul et al. 1987; Reisinger et al. 1990; Hsia et al. 2013), but we really know little about either the compression of the air sac or the function of the tracheal spiracle. It is likely that opening and closing of this spiracle is regulated, perhaps in the same way that the book lung spiracles appear to be regulated. Detailed studies of this could tell us much about the role of the tracheae. In other spiders a *tracheal dilator* muscle is either present (*Latrodectus*, Whitehead & Rempel 1959) or absent (*Araneus*, Robinson & Paim 1969).

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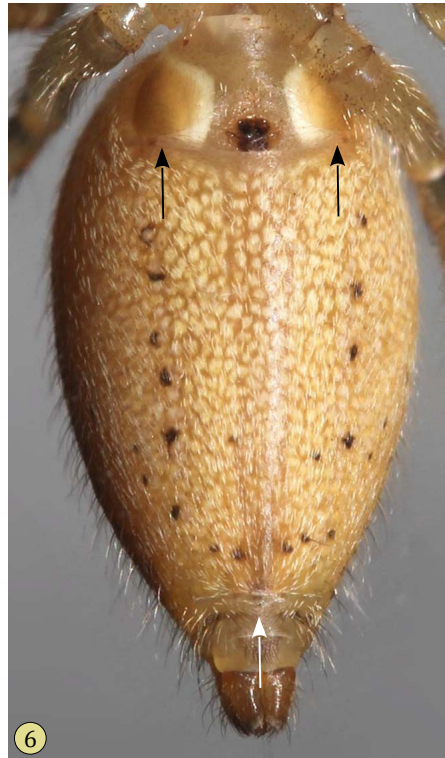
Appendix 1. Ventral views of some North American jumping spiders
Arrows indicate positions of the two pulmonary spiracles and the tracheal spiracle (Figure 13).



Figures 13.1-13.2. Adult male *Lyssomanes viridis* (Walckenaer 1837), Greenville County, South Carolina.



Figures 13.3-13.4. Adult female *Lyssomanes viridis*, Greenville County, South Carolina.



Figures 13.5-13.6. Adult female *Colonus puerperus* (Hentz 1846), Greenville County, South Carolina.



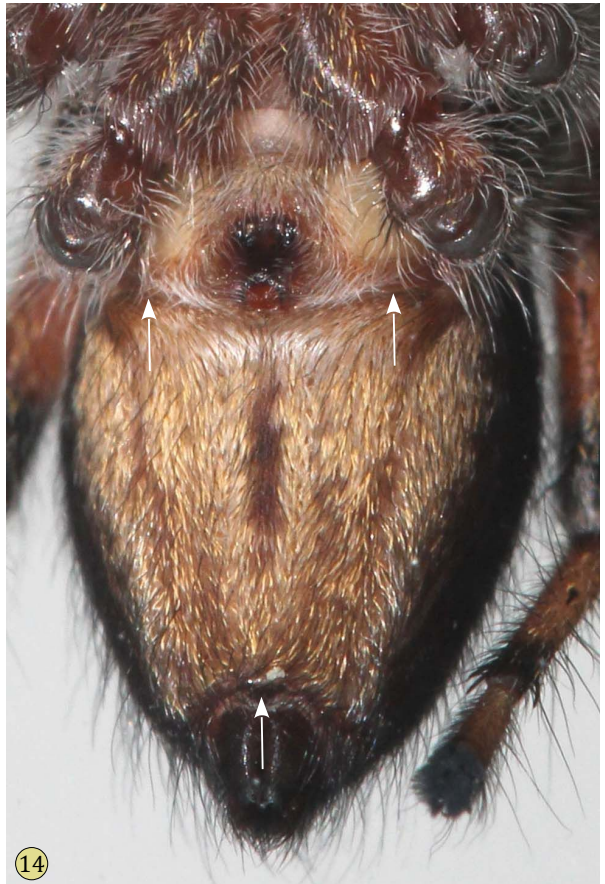
Figures 13.7-13.8. Adult female *Colonus sylvanus* (Hentz 1846), Greenville County, South Carolina.



Figures 13.9-13.10. Adult female *Phidippus arizonensis* Peckham & Peckham 1883, Cameron County, Texas.



Figures 13.11-13.12. Adult female *Phidippus californicus* Peckham & Peckham 1901, Mexico.



Figures 13.13-13.14. Adult female *Phidippus cardinalis* (Hentz 1845), Greenville County, South Carolina.



Figures 13.15-13.16. Adult female *Phidippus clarus* Keyserling 1885, Greenville County, South Carolina.



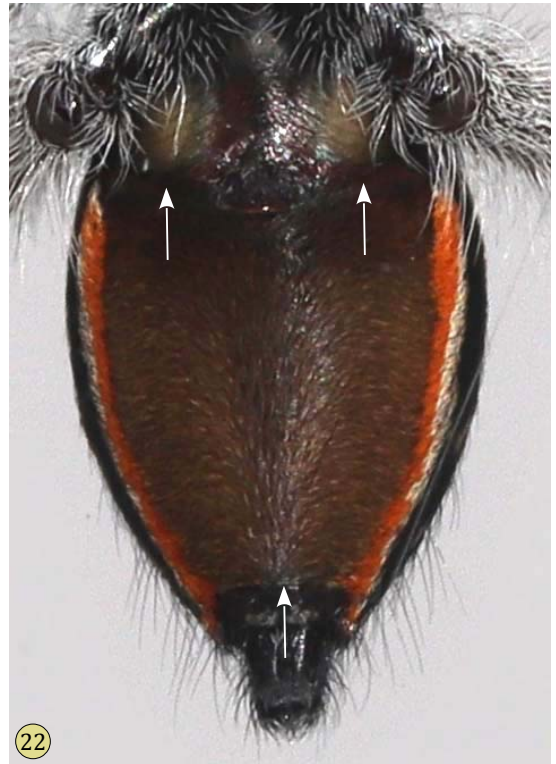
Figures 13.17-13.18. Adult male *Phidippus comatus* Peckham & Peckham 1901, Oregon.



Figures 13.19-13.20. Adult female *Phidippus comatus*, Oregon.



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Figures 13.21-13.22. Adult male *Phidippus pacosauritus* Edwards 2020, Mazatlán, Sinaloa, Mexico.



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24

Figures 13.23-13.24. Adult female *Phidippus pacosauritus*, Mazatlán, Sinaloa, Mexico.