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Some observations on the physiology of living *Lyssomanes viridis* which should apply to the Araneae in general

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Original pagination is retained for reference in this republication of the article originally published as: Hill, D. E. 1977 Some observations on the physiology of living *Lyssomanes viridis* which should apply to the Araneae in general. *Peckhamia* 1 (3): 41-44. Figure 2 has been replaced with an available color photograph of the same spider. A note has also been added at the end of this paper to illustrate several important features of book lung structure described in the text.

1. Original text with pagination

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SOME OBSERVATIONS ON THE PHYSIOLOGY OF LIVING LYSSOMANES VIRIDIS WHICH SHOULD APPLY TO THE ARANEA IN GENERAL. D. E. Hill

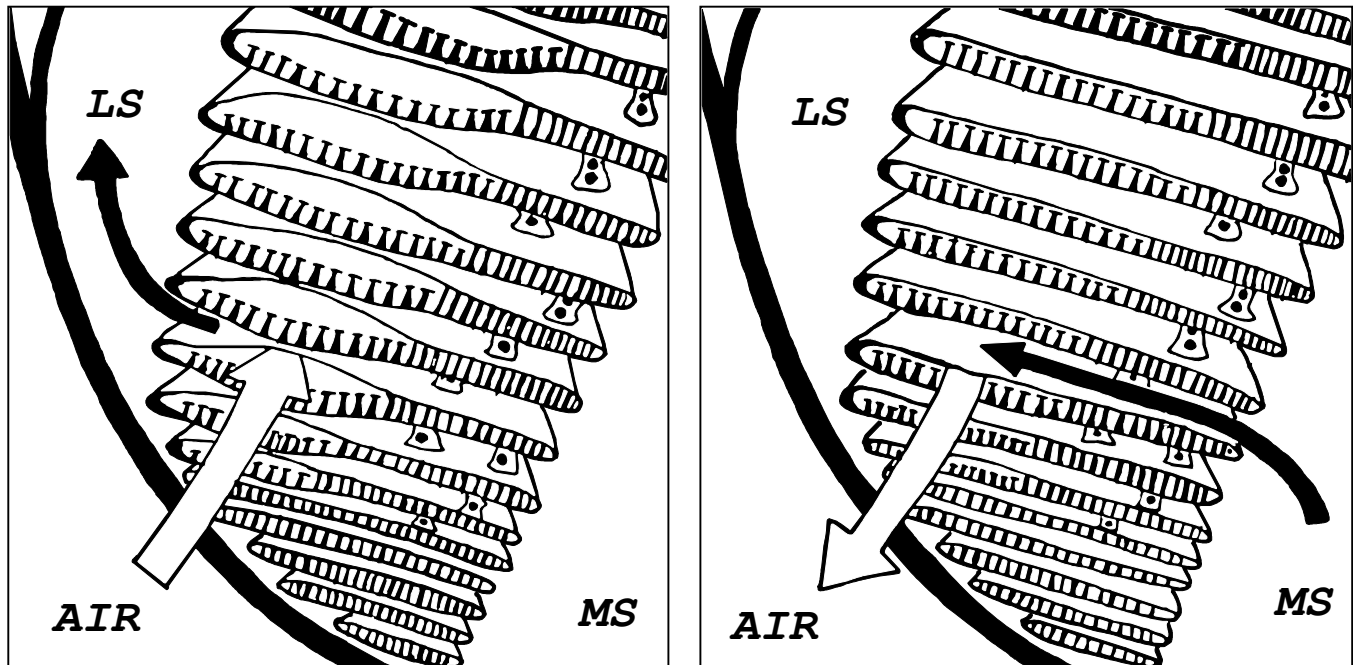
Recently I examined the structure of the cryofractured book lung of Phidippus audax with a scanning electron microscope. Each book lung is essentially a stack of flattened air-sacs, or lamellae, which project anteriorly into the lateral hemolymph space of the anterior opisthosoma. Each lamella is roughly triangular in shape. Hemolymph flows across each lamella from the medial to the lateral side (Fig. 1). Air enters the lamellae from the third, posterior side, after passing through a network of irregular cuticular struts (air filter) which lines the atrium of the book lung. The thin walls of each lamella are joined by rigid struts near the medial side, and the intra-lamellar air space cannot be expanded or compressed in this region. Toward the posterior and lateral sides, however, the two walls of each lamella are not joined. Here the inner surface of the ventral (or ventro-lateral) wall is covered with buttressed studs, while the opposing dorsal (dorso-medial) wall is completely smooth. Thus a large portion of each lamella is capable of considerable expansion, and the residual (minimal) air volume is dictated by the height of these studs (about 3 μm). S.J. Moore (1976) describes a similar structure for some other

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spiders (Araneus, Argiope, Argyroneta, and Tegenaria). This distinctive structure demands a functional explanation.

In this regard, I have been able to observe regular movement of the book lung lamellae directly, through the transparent lateral wall of the opisthosoma of Lyssomanes viridis (Fig. 2). An unrestrained adult female, resting on a near-vertical surface after feeding, was observed under a binocular microscope at a magnification of 144 X. The spider was carefully tilted until I was able to look directly across the surface of the lamellae (This near-lateral view is about 15 degrees above the lateral view, and both lighting and the fortuitous placement of leg IV by the spider are critical). In this position, the rapid movement, up and down, of each series of lamellae in unison is evident. Each upward movement of the lamellae coincides with the pulsatile flow of hemolymph toward the readily visible pulmonary vein, as the heart contracts at a rate varying from 150 to 210 cycles/minute. After completing this observation, I discovered that V. Willem

Fig. 1. The hemolymph bellows hypothesis for book lung ventilation: Schematic transverse sections of the left book lung, as seen from the rear. Hemolymph of the medial sinus (MS) flows between the lamellae (flattened air-sacs) of the book lung to the lateral sinus (LS), then ascends dorso-medially to the heart via the pulmonary vein. Left: The lamellae are inflated with air as hemolymph is pulled out of the inter-lamellar spaces by the contracting heart. Right: With relaxation of the heart, hemolymph enters the book lung from the medial sinus to compress the lamellae.



(1918) had observed the same synchrony of heartbeat and lamellar movement in *Pholcus phalangioides*; I have subsequently repeated this observation with a local pholcid. In *Lyssomanes*, the visible movement is greatest for the dorsal lamellae, nearest to the pulmonary vein. The ability of the heart to move the lamellae in this manner suggests that the suction force applied to the thin lamellar walls with each heart beat should be able to lift these walls apart, much as one would inflate a bellows, thereby inflating the lamellae. Stewart and Martin (1974) recorded the requisite decline of pressure in the pulmonary vein of a spider with each contraction of the heart. At this size scale the

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pull of the contracting heart appears to be conveyed as an impulse through the viscous hemolymph. Fluid pressure within the medial sinus (Fig. 1) should immediately force a distension of the inter-lamellar spaces, and a deflation of the lamellae, prior to the next contraction of the heart. A less regular movement of the lamellae was also observed in 15 day embryos of *L.viridis*.

This characterization of the book lung as a passive hemolymph bellows, driven indirectly by the heart beat, may be generally applicable to the Araneae, if not the Arachnida. The book lung, rather than merely representing a curiously primitive and inefficient way of increasing the surface area available for gaseous diffusion (which it does), is, in my opinion, a very successful device for utilizing the flow of hemolymph to power ventilation of the respiratory surface. This use of hydraulics to achieve physical movement is a general feature of the Arachnida.

Fig. 2. Adult female *Lyssomanes viridis* (Walckenaer 1837) collected by D.B. Richman in April of this year in magnolia, Martin County, Florida. These spiders typically lurk in rudimentary retreats on the underside of magnolia leaves. The actual length of this livid green spider is 7 mm. The scales of the optic quadrangle are bright red and white. The narrow front of the prosoma (corresponding to the extreme posterior position of the ALE), the relatively long legs, and the extreme flexibility of the tarso-metatarsal joint are all unusual for a salticid.



Several other observations of interest are also possible with *Lyssomanes*. Occasionally one can observe the opening and closing of the spiracle, as well as a certain amount of movement of the posterior wall of the vestibule or atrium of the book lung. This may be associated with an irregular rhythm of tidal flushing of the book lung. The heartbeat is readily observed, although rapid movement of hemolymph through the appendages is more difficult to see and requires the combination of concentrated effort with appropriate trans-illumination. Movement of the pigmented eye tubes of the AME is easily observed from above, as well as directly through the lenses.

With an individual that has fed recently, one can observe peristaltic waves of the midgut where it passes through the pedicel, between the book lungs. The constant churning of fluid, particles, and droplets within the extensive midgut diverticula of the opisthosoma is also readily observed, definitely indicating the presence of contractile elements in these structures. While the spider is feeding, almost-violent pulsations of diverticula in the space lateral to the AME may be synchronized with movements of the sucking stomach. The dynamic qualities of digestion are apparent.

Perhaps one of the most impressive observations which one can draw from looking at transparent spiders, including *Lyssomanes*, is the extreme translucidity of internal structures. This includes both nerves and muscle, as well as the individual cells of the digestive diverticula containing darker droplets. One is greatly impressed by the important distinction between the fixed artifacts of a histological preparation and the dynamics of a living, fluid structure.

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2. Additional comments with respect to the structure and function of salticid book lungs

There are two points of great interest with respect to salticid (and most likely other spider) book lungs that I think have been clearly established: 1) the lateral portions of the lamellae of at least some, and perhaps all, species move actively in synchrony with the heartbeat, and 2) air spaces within each lamella occur in two varieties, those that are fixed in volume, and those that are distensible. The *hemolymph bellows* hypothesis presented in this republished paper proposed that this distension actually took place, and that it was driven by the heart beat by means of a cyclic flux in hemolymph pressure and flow.

Since 1977, there has been limited work with respect to this hypothesis, notably the supportive studies related to the scaling of lung structures and related metabolic requirements by Anderson and Prestwich (1980, 1982). Foelix (1996) cited some larger spider studies, and concluded that *diffusion* (and not ventilation) was the primary mechanism at work. Of course, diffusion between air and fluid, through a surface, is key to the function of *all* lungs, but the book lung is hardly a passive organ with respect to ventilation. Unlike the tracheae which provide their own *gas line* transport, the book lungs rely on a large and powerful fluid pump (the heart), in conjunction with hemocyanin protein complexes (e.g., Ballweber et al, 2002), to transport O₂ and CO₂ throughout the body.

One published picture (Foelix 1996, Figure 56, page 63; Figure 3 here) shows only a portion of the book lung where the lamellae *are* distensible. A more informative picture is shown here in Figure 4, for comparison. This picture shows clearly the presence of both fixed and distensible air spaces in the salticid book lung.

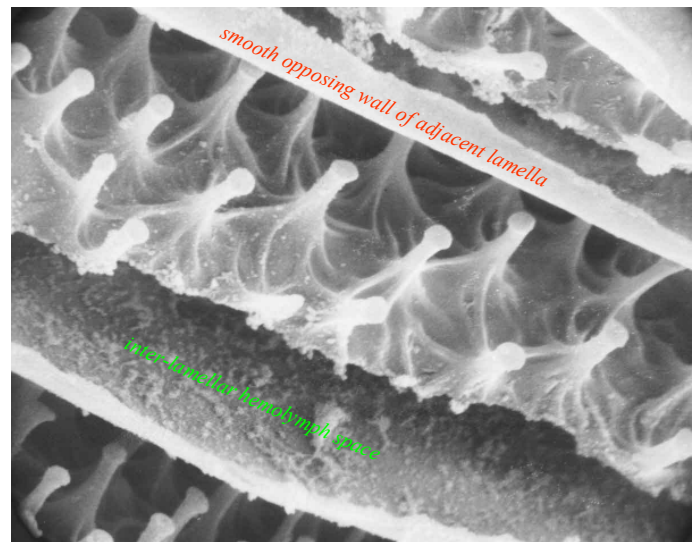


Figure 3. Distensible air spaces separated by pegs with rounded caps, from cryofractured book lung of adult male *Phidippus audax*. Note the buttresses that support each peg. The opposing wall of the adjacent lamella is completely smooth and devoid of features.



Figure 4. Transition between distensible and fixed intra-lamellar air spaces, from cryofractured book lung of adult male *Phidippus audax*. Note the greater height of the fixed struts or separators at the point of transition. Hemolymph should be forced to move faster as it moves into the narrower fluid space at the transition point.

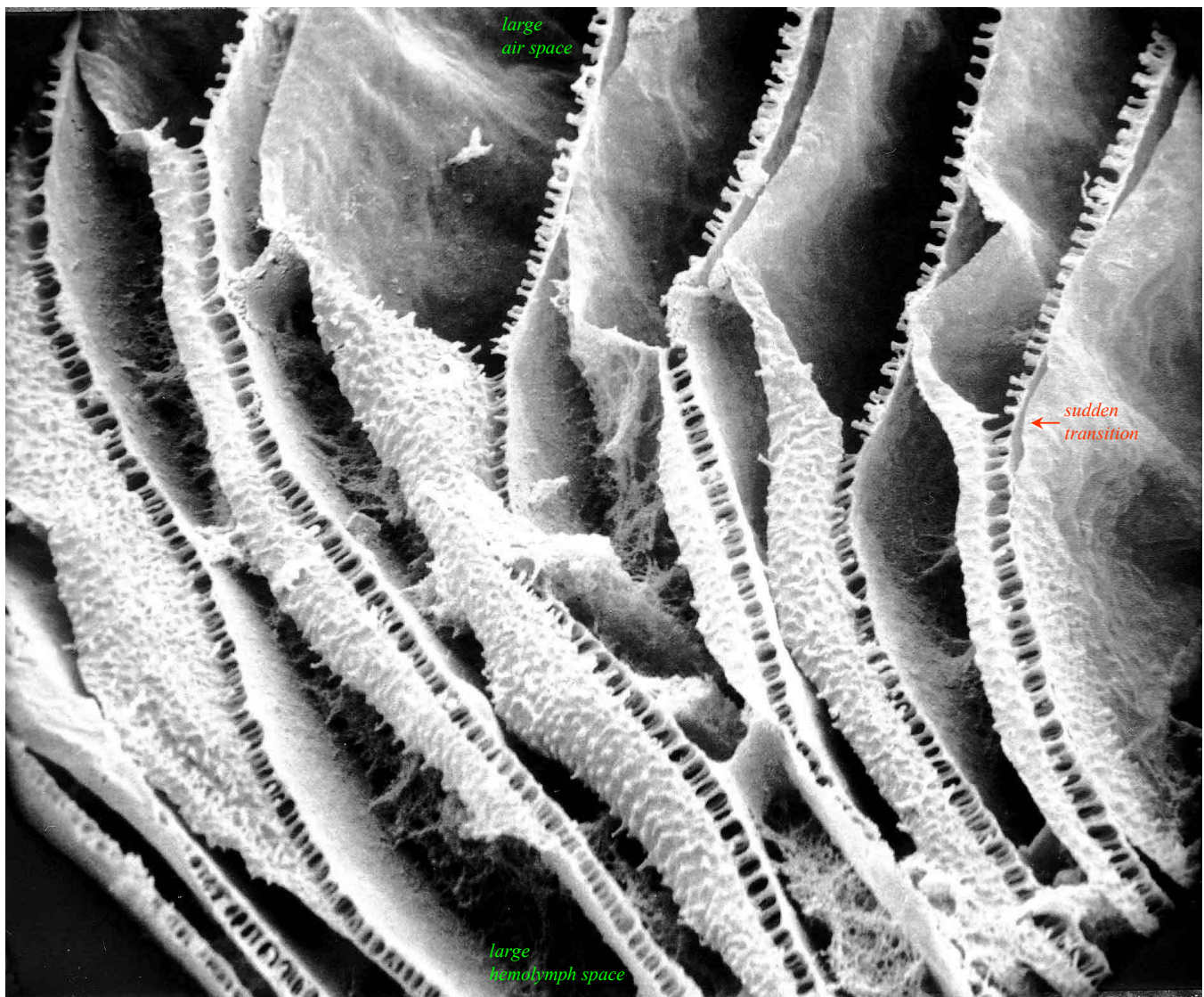
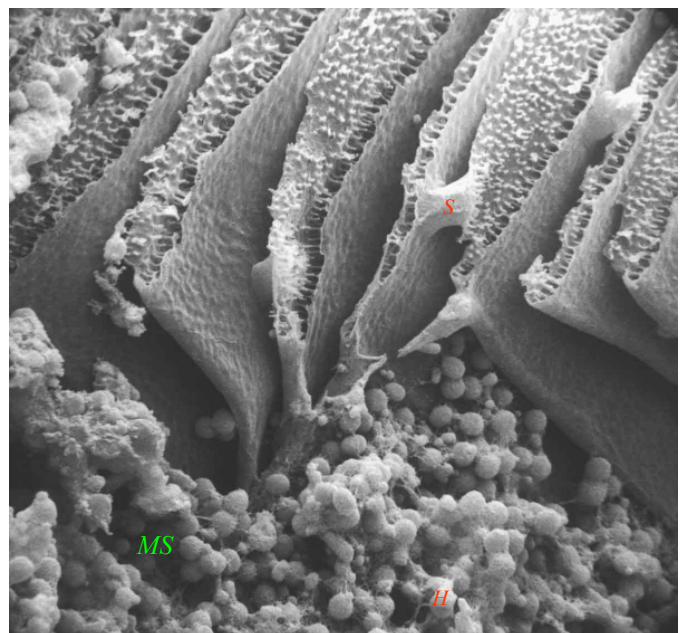


Figure 5. (right) Larger view of transition between distensible and fixed intra-lamellar air spaces, from cryofractured book lung of adult male *Phidippus audax*. Flow of hemolymph is from the bottom to the top. Here the structural transition from large hemolymph channels separated by thin lamellae (bottom) to potentially very large air spaces bounded by thin walls is obvious.

This sudden transition between fixed and distensible portions of the book lung is even more evident at the larger scale depicted in Figure 5. The extremely thin and unsupported walls of the distensible portions of these lamellae must be capable of considerable movement during rapid cycles of hemolymph pressure change. It is not hard to imagine how a pressure vacuum created by contraction of the heart could be associated with expansion of the air chambers that are closest to that heart.

Air spaces of the lamellae are relatively small and fixed in the medio-ventral direction where hemolymph moves from the medial sinus (MS) into the broad channels between these plates (Figures 6, 7).

Figure 6. Fixed air spaces of lamellae where the book lung meets the medial sinus (MS), from cryofractured book lung of adult male *Phidippus audax*. Note the many hemocytes (H) in the hemolymph-filled space of the medial sinus, and the paired spacer cells (S) connecting adjacent lamellae.



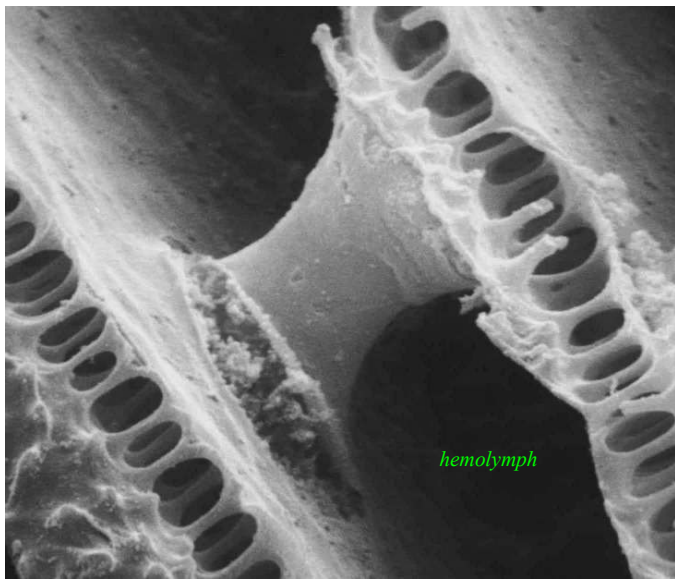


Figure 7. Detail of hemolymph space between the fixed air spaces of two adjacent lamellae, from cryofractured book lung of adult male *Phidippus audax*. The separator in the hemolymph space at center actually consists of two joined cells, one associated with each of the lamellae. Note how wide the hemolymph space is in this part of the book lung, relative to the smaller fixed intra-lamellar air space.

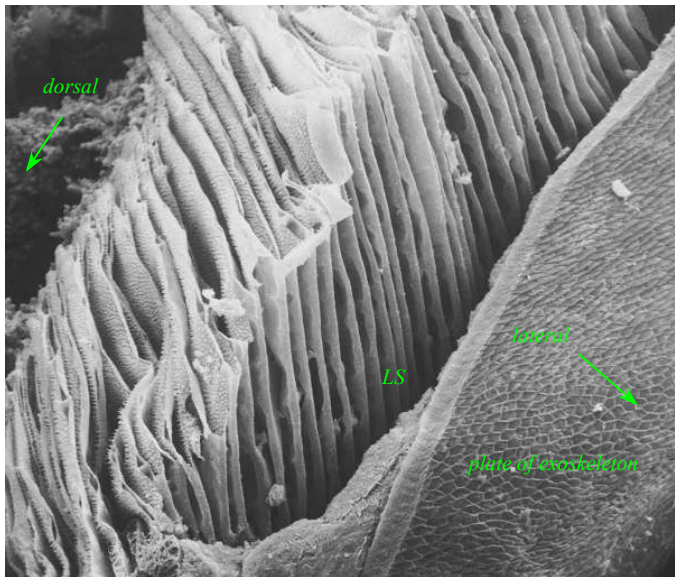


Figure 8. Distensible air spaces of dorsal and lateral portions of lamellae, from cryofractured book lung of adult male *Phidippus audax*. Note the thick body wall (plate) bounding the lateral sinus (LS).

Laterally and dorsally (Figure 8), the air spaces of the lamellae are distensible within the lateral sinus (LS), also bounded by a hard wall of the exoskeleton that resists deformation. It appears as if this thick-walled lateral chamber is designed to direct the full force of hemolymph pressure against the very thin walls of the distensible lamellae. As shown in Figure 10, each lamella can be viewed as a flattened, triangular, air-filled pocket. One side faces the open spiracle (bidirectional movement of air molecules), one side faces the medial sinus (hemolymph input), and one side faces the lateral sinus (hemolymph output).

The point of entry into the lamellae is shown in Figure 9. The irregular framework near the spiracle can be compared to a cigarette filter.

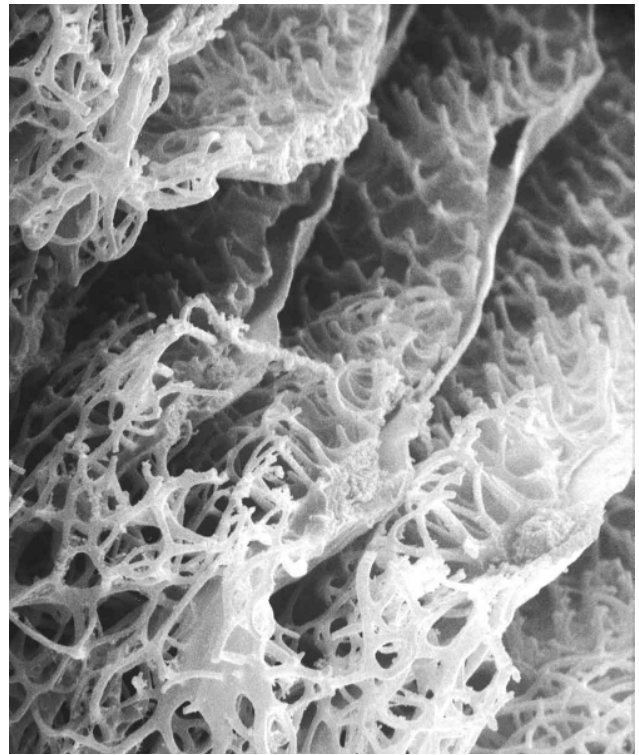


Figure 9. Air entry into distensible portion of lamellae, from cryofractured book lung of adult male *Phidippus audax*. Note the mesh work of the air filter that separates the lamellae of the book lungs from the vestibule (lower left).

Cycles of heart contraction and expansion are closely tied to movement of hemolymph through the book lungs (Figure 11). I am not aware of any studies that relate air pressure to hemolymph pressure, but it is clear from the direction of hemolymph flow that hemolymph spaces in the book lungs are cyclically subject to greater pressure medially, and less pressure laterally. Cycles of pulsatile flow can occur very quickly in salticids (hundreds of cycles per minute). Each increase in fluid flow between adjacent lamellae greatly reduces fluid pressure perpendicular to those lamellae (*Bernoulli's principle*; as one example, a rapid stream of water flowing down a shower curtain pulls that curtain *inward*). Can a combination of the pulsatile fluid pressure gradient associated with the heartbeat, and the resultant hemolymph flow, pull in the thin walls of these lamellae? Does function follow form here?

The opening and closing of the spiracles (Figure 12) has been associated with tidal flushing of the book lungs (Anderson and Prestwich 1980). Given the much greater extent of pulsatile hemolymph movement through the book lungs, I would think that the *hemolymph bellows effect* would be much more important.

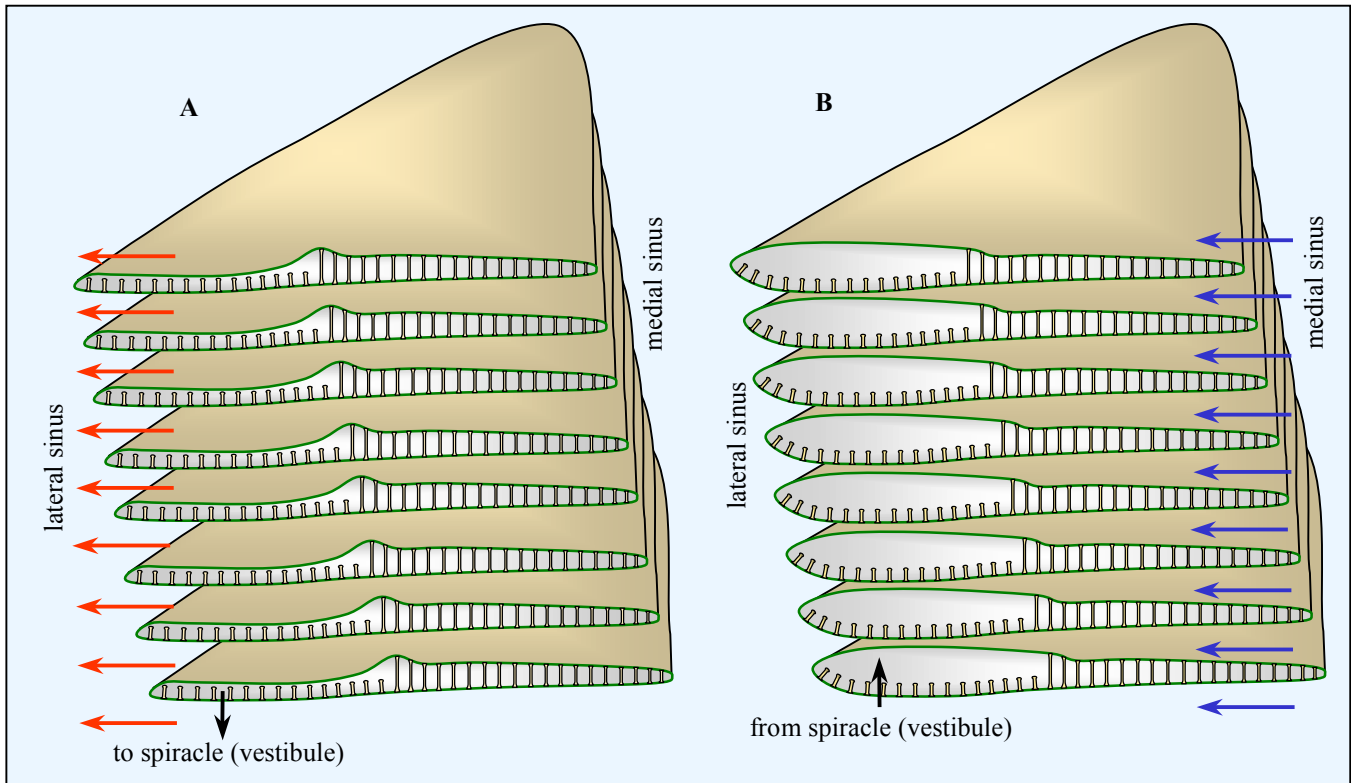


Figure 10. Schematic view of book lung, from the rear. As shown here, each lamella can be viewed as a flattened, triangular air pocket, bounded by the vestibule. A: Hypothetical view of lung during (heart) contraction cycle, when it is filled with hemolymph and the distensible air spaces have collapsed, expelling air from the lung. B: Hypothetical view of lung during (heart) expansion cycle, showing how distensible air chambers could be inflated by vacuum fluid pressure associated with rapid expansion of the heart.

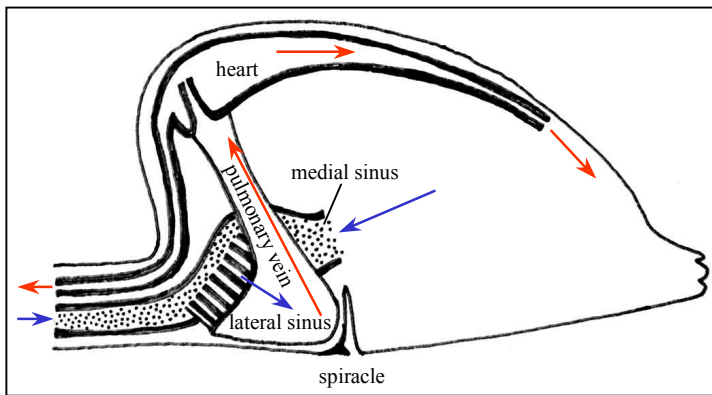


Figure 11. Relationship of heart to the book lungs (lateral view of telson and opisthosoma). Expansion of the heart pulls in hemolymph from the book lungs via a pulmonary vein on each side of the spider. Contraction of the heart drives hemolymph into the body of the spider and also back into the book lungs by way of the medial sinus.

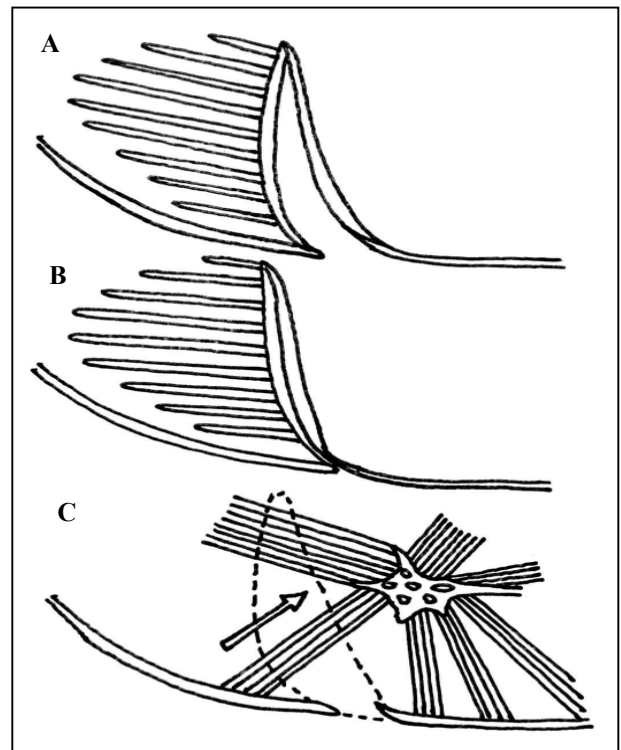


Figure 12. (right) Relationship of the spiracle and associated vestibule (atrium) to the book lung. A: Open spiracle and vestibule (entry chamber or air-sac) allows free air flow or diffusion into and out of the book lung. B: Closed spiracle and vestibule. C: Schematic view of muscles associated with closure of the spiracle. These are attached to an internal skeletal element or cartilage within the telson (opisthosoma) of the spider.

Additional References Cited with this Commentary:

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