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Book lung development in juveniles and adults of the cobweb spider, *Parasteatoda tepidariorum* C. L. Koch, 1841 (Araneomorphae, Theridiidae)

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ABSTRACT

Light and transmission electron microscopy were used to study the development of new book lung lamellae in juvenile and adult spiders (*Parasteatoda tepidariorum*). As hypothesized earlier in a study of embryos, mesenchyme cells dispersed throughout the opisthosoma (EMT) are a likely source of precursor epithelial cells (MET) for the new lamellae. The precursor cells in juveniles and adults continue many of the complex activities observed in embryos, e.g., migration, alignment, lumen formation, thinning, elongation, and secretion of the cuticle of air channel walls and trabeculae. The apicobasal polarity of precursor cells for new channels is apparently induced by the polarity pattern of precursor cells of channels produced earlier. Thus, new air and hemolymph channels extend and continue the alternating pattern of older channels. At sites more distant from the spiracle and atrium, new channels are usually produced by the mode II process (intracellular alignment and merging of vesicles). These air channels have bridging trabeculae and are quite stable in size throughout their length. At sites closer to the spiracle and atrium, new channels may be produced by mode I (coalescence of merocrine vesicle secretion). This raises the hypothesis that structural and functional differences in mode I and II channels and differing oxygen and fluid conditions with distance from the spiracle and atrium determine the mode of formation of new channels. Observations herein support an earlier hypothesis that there is some intercellular apical/apical and basal/basal affinity among the opposed surfaces of aligned precursor cells. This results in the alternating pattern of air channels at the apical and hemolymph channels at the basal cell surfaces.

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1. Introduction

Light (LM) and transmission electron microscopy (TEM) were used herein to continue a comparative investigation of the development of book gills in the horseshoe crab (Farley, 2010, 2012) and book lungs in the scorpion (Farley, 2005, 2008, 2011) and spider (Farley, 2015, 2016). The spider species of these investigations is very prolific, has a relatively short life cycle and can be maintained in a laboratory colony (McGregor et al., 2008; Miyashita, 1987; Hilbrant et al., 2012). This has enabled some detailed analysis of cellular activity as lamellae are formed in embryos and early postembryonic stages (Farley, 2015, 2016) and also in the present investigation as the book lungs are enlarged in juveniles and adults. In these chelicerate respiratory organs, epithelial precursor cells with apicobasal polarity align in rows and gradually form a polarized planar tissue with hemolymph channels that alternate with air or water channels. These book-like structures are a model system for studies of tissue morphogenesis (McGregor et al., 2008; Hilbrant et al., 2012; Farley, 2015, 2016) and gene expression (e.g., Damen et al., 2002; Simonnet et al., 2006; Pechmann et al., 2010), and information is provided for hypotheses about evolutionary relationships (e.g., Dunlop, 1998, 2010; Scholtz and Kamenz, 2006; Kamenz and Prendini, 2008; Dunlop and Lamsdell, 2017)).

At least in some species studied so far, spider embryos have a small bilateral cluster of initial temporary (IT) lamellae that form in the second opisthosomal (O2) segment just posterior to the O2 limb buds (Wolff and Hilbrant, 2011; Mittmann and Wolff, 2012; Farley, 2016). There is variable expression of these lamellae among the species, and if present they are replaced by advanced embryo (AE) lamellae that develop within the O2 limb buds (Pechmann et al.,

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2010; Farley, 2016). The distal end of the O2 limb buds joins with the ventral surface of the O2 segment, and the limb bud/book lung tissue is internalized by covering with an epidermal layer.

Farley (2016, Fig. 16) provided evidence and a proposal that cells of the opisthosomal epidermis in spider embryos undergo an epithelial-to-mesenchyme transition (EMT) and migrate anteriorly, forming entapophyses (slender stands of cells and reticular fibers). There may be cuticular invagination at some entapophysis sites leading to muscle (Lankester et al., 1885), but entapophyses are often just cells and fibers from proliferation and inward migration of epidermal cells. In addition to the mesoderm that is produced during gastrulation (Mittmann and Wolff, 2012), entapophyses are a likely source of mesenchyme cells dispersed throughout the abdomen where they provide precursors for developing organs. Such EMT is a basic feature of metazoan embryogenesis as described in recent reviews (e.g., Lee et al., 2006; Acloque et al., 2009; Thiery et al., 2009; Lim and Thiery, 2012). Entapophyses are reported to be the source of cells for the lateral tracheae in the O3 segment of spider embryos (Purcell, 1909, 1910).

In histological sections of spider embryos, an entapophysis is commonly seen attached at the base of each O2 limb bud, a site which is also the medial-posterior margin of a developing book lung (Farley, 2016). Here, the entapophysis cells are hypothesized to undergo a mesenchyme-to-epithelial transition (MET) and become book lung precursors within the limb bud; the entapophysis/mesenchyme cells may also induce some limb bud cells to become precursors. Whatever their origin, the precuror cells align and start producing lumina that become the alternating air and hemolymph channels.

In spider embryos, the apicobasal polarity of the book lung precursor cells becomes evident as the cells begin to form lumina (Farley, 2015, Fig. 16; 2016). In electron micrographs, clear spaces for the primordial air channels develop at the opposed apical ends of aligned precursor cells while hemolymph spaces develop usually later at the basal end of the precursor cells.

Electron micrographs also show that different modes of lumen formation are used, depending on location and probably other conditions within the primordial book lung (Farley, 2015, Fig. 16, 2016). Especially at the posterior end of the book lung where the spiracle, atrium and earliest lamellae are formed, the lumina may be produced by *cord hollowing* among the aligned cells (Andrew and Ewald, 2010). This results from the extracellular coalescence of merocrine secretion from vesicles. This process, labeled as mode I by Farley (2015, Fig. 16) is also used to increase the size of the air channel as the molt removes the earlier air channel cuticular wall and trabeculae (Farley, 2016).

Another very common mode of lumen formation is *cell hollowing*, the intracellular alignment and merging of vesicles (Andrew and Ewald, 2010). This was labeled as mode II by (Farley, 2015, Fig. 16, 2016). The mode II process may be used for the initial formation of some lamellae in the embryo and also, as shown herein, for lengthening and adding new lamellae as the book lung is increased in size during and after the molt. New lamellae are most commonly mode II at the anterior, dorsal and medial aspects of the book lung, at sites more distant from the spiracle and atrium.

Mode III is the development of thin spaces between aligned precursor cells, possibly by diffusion of fluid in response to an osmotic gradient (Farley, 2015, 2016). This is commonly evident in the initial development of hemolymph channels. Cell death is also likely involved in clearing space for passage of air and hemolymph since cell debris is often seen in developing spiracles, atria and air and hemolymph channels.

As hypothesized earlier (Farley, Fig. 16), book lung precursor cells align in rows and have some type of affinity between their opposed apical surfaces and also their opposed basal surfaces. The apical surfaces produce air channels while the hemolymph channels are formed at the basal surfaces. Results herein show that cells with these affinities may be able to induce similar properties in nearby cells, so there is propagation and repetition of the alternating pattern of air and hemolymph channels.

The various modes of lumen formation observed in earlier stages (Farley, 2015, 2016) are continued in juveniles and adults as the book lungs are lengthened and made wider with new-growth lamellae. The precursor cells appear to come mainly from mesenchyme cells dispersed within the opisthosoma and at the periphery of the book lung chamber. As these mesenchyme cells become precursor cells and part of the book lung, their polarity and alternating channels continue the pattern in the earlier adjacent channels. The initial round or ovate precursor cells undergo striking changes in shape and behavior as they become very thin and elongate and part of the air channel walls with supporting cuticle and trabeculae. These cuticular structures are replaced during the molt while the cellular pillar trabeculae in the hemolymph channels continue development.

2. Materials and methods

2.1. Experimental animals

A culture of *Parasteatoda tepidariorum* was maintained with procedures like those described earlier for this species (Mittmann and Wolff, 2012; Farley, 2015, 2016). Egg sacs and newly hatched spiderlings were kept in small petri dishes at 25–30 °C. Advanced juveniles and adults were separated into individual plastic containers (280 ml) with paper on the bottom and a partially opened bottom of a styrofoam cup for cover, web attachment and support for a small pad of moist paper. These spiders were maintained at 22–24 °C with a 12:12 h photoperiod. They were fed, containers cleaned and the papers changed once each week. Spiderlings were given a flightless strain of freshly killed fruitflies (*Drosophila hydei*) and small crickets while juveniles and adults were given freshly killed crickets of larger size. In experiments with long and short photoperiods, Miyashita (1987) reported four to six molts in 30–80 days from cocoon to adult in the males of this species while there are five to seven molts in 40–100 days for females.

2.2. Histology

A fine pin was inserted into the prosoma of juvenile and adults specimens, and each individual with inserted pin was immersed in physiological saline (Schartau and Leidescher, 1983). Fine forceps and scissors were used to separate the book lungs from nearly all the exoskeleton, and a pin was inserted in any remaining cuticle at the posterior end of the book lung. The pins were used to secure the specimen and prevent floating of excised lung tissue with air inside. The pinned tissue was immersed in Bouin's fixative. After 12–24 h, the embryos were washed in physiological saline (Schartau and Leidescher, 1983), removed from the pins, dehydrated in a graded sequence of ethanol and embedded in paraffin. Sections (8 μm) were stained with Harris' hematoxylin and eosin Y. Bouin's fixative, staining solutions and procedures were obtained from American Master Tech Scientific, Lodi, CA.

2.3. Electron microscopy

The book lungs were dissected in physiological saline (Schartau and Leidischer, 1983) as described above. The pinned book lung tissue was immersed in glutaraldehyde fixative (2–4 °C) for 12–24 h. The fixative consisted of 2% glutaraldehyde and 0.1 M

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