Functional Implications of the Pulmonary Microcirculation*
An Update
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The microscopic anatomy of the pulmonary circulation was reviewed, comparing the evidence for two competing models, the sheet-and-post paradigm and the tubular paradigm. Implications of the two paradigms were analyzed for function, including flow, recruitment, distension, and diffusion. We conclude that the pulmonary microcirculation is not essentially different from the systemic microcirculation except that two layers of tubular capillaries are arranged on a central layer of connective tissue, the alveolar wall. We find no morphologic basis or theoretic advantage for the sheet-and-post concept.

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The pulmonary microcirculation was thought to be composed of the same components (i.e., capillaries) as the systemic circulation from the time of Malpighi in 1661 until 1969, when Fung and colleagues began publishing their series of articles asserting that the pulmonary alveolar microcirculation consisted of sheets separated by posts.

**The Sheet-and-Post Paradigm**

Fung et al emphasized a new concept of sheet flow, but they explicitly rejected tubules as the fundamental unit of the pulmonary microcirculation; they asserted that their sheet-and-post model was solidly based on morphometry. They compared alveolar microcirculation to a “parking garage with floor, ceiling, and intervening posts.” However, their morphometry was based on a light microscopic study of latex casts with a distending pressure of 15 mm Hg, which appear overstressed (see Fig 1 in reference 3). In general, light microscopy has relatively poor resolution and a shallow depth of field.

They discarded Poiseuille’s law for flow, because they regarded capillary segments as wider than long, although they did not actually measure the length, and their own diagram shows sheets that are longer than wide (see Fig 27 in reference 8 and also reference 2). For their calculations, they used the measurements of Weibel, who reported length as 1.3 to 1.6 times greater than diameter. Their formula for sheet flow was: Flow = h/μ, where h is the height of the posts separating the sheets, and b = (4 μL)(compliance/surface area), where μ represents viscosity and L represents the length of a segment.

According to Sobin et al, sheet thickness was linearly related to distending pressures, but their intercept value for zero pressure was 4.3 μm, which would not be compatible with collapse of septal capillaries under zone I conditions. In fact, their “posts” would prevent complete collapse of capillaries (“sheets” in their paradigm) and would create a “circus tent” morphology in zone I conditions, which Fung and Yen acknowledged.

Although the species originally used by Fung and Sobin was the cat, they asserted that “all pulmonary alveolar septa in adult mammalian lungs are similar. Each septum contains one single sheet of capillary blood vessels and is exposed to air on both sides.” The issue of a single versus a double layer of microcirculation in the alveoli is of considerable embryologic and functional significance.

**Our Anatomic Findings**

In our scanning electron microscopic study of pulmonary microcirculation, we used latex casts in live, anesthetized rats. The casts were fixed at physiologic distending pressures, 10 cm H2O, in relation to airway pressures. After tissue digestion, the vascular replicas were coated and scanned (Fig 1).

We found that there were two types of microvasculature in the lungs: (1) the marginal microcirculation, consisting of low-density, long, tubular capillaries at the pleural surfaces and in the peribronchial spaces; and (2) the alveolar microcirculation. The latter is
composed of a tight meshwork of intersecting tubules in two layers, on either side of the alveolar septum, with frequent interconnecting branches (Fig 2).

We concluded that the basic component of both types of vasculature is tubular, not sheets separated by posts. The mean diameters for the capillaries of the two types of vasculature were 5.5 ± 0.2 for the marginal type and 5.8 ± 0.2 μm for the alveolar type (not significantly different). Although the alveolar capillaries are of variable length, the length is greater than the diameter, which indicates that Poiseuille's law would not be invalid if applied to this circulation. The major differences between these two vascular types, marginal and alveolar, were the greater density of the alveolar capillaries and their double layer. We did not detect a predominance of hexagonal geometric forms in the alveoli, contrary to Weibel's prediction.10

The Literature Concerning Morphology

Embryology

Burri12 followed the development of rat lung after birth, progressing from no alveoli, only saccules, to alveoli after four days. He described the primary septa at birth as having two layers of capillaries. For the subsequent septa which develop into mature alveoli, he postulated two possible developmental models, both of which had two layers of capillaries; one model had fusions between the two layers, and one model did not. On our scanning electron micrographs,11 the connecting vessels or fusions between the two layers are quite frequent (Fig 2).

A major problem for the post-and-sheet theory is the organogenesis of the two types of pulmonary capillaries, the marginal and the alveolar. The marginal vessels are unequivocally composed of conventional capillaries (Fig 1); how the sheet-and-post microcirculation would merge with these capillaries is difficult to conceive and has not been explained by its proponents. The two types of lung capillaries were described by Miller13 over 50 years ago. Miller clearly regarded both types as being formed of tubules, with greater density in the alveolar microcirculation.
Double or Single Layer of Alveolar Capillaries?

Ryan\textsuperscript{14} showed that there was a layer of capillaries on both sides of the mature alveolar wall. To determine this issue of one versus two layers of capillaries with light microscopy, he emphasized that serial sections with careful orientation were necessary; a single microscopic section proves nothing about one versus two layers, given the complexities of the alveolar wall. Ryan also found that the connective tissue in the center of the alveolar wall is continuous with the perivascular cuff tissue and with the lymphatics. This provides a potential space for the accumulation of fluid and a pathway for the lymphatics, consistent with clinical findings from x-ray and histologic studies in the early phases of pulmonary edema. In the sheet-and-post model, it is not clear how the interstitial fluid could migrate to the lymphatics.

In the sheet-and-post concept, there is a single sheet with structural elements on both surfaces. This would require that both surfaces be equally thick, a disadvantage for diffusion (see below). DeFouw and Shumko\textsuperscript{15} found that even the endothelium on the alveolar side was thinner than the endothelium on the septal side, which contained the interstitial supportive tissue. Miller\textsuperscript{13} and von Hayek\textsuperscript{16} also concluded that a double layer of alveolar capillaries exists.

Elastic Tissue Distribution

The distribution of elastic tissue in the alveoli is not consistent with the sheet-and-post model. Scanning electron microscopic studies after partial digestion reveal elastic fibers that branch continuously in a reticulum, rather than radiating from focal points or "posts."\textsuperscript{17}

Dimensions

Weibel\textsuperscript{18} reported an average capillary diameter of 6.0 \( \mu \)m in the human lung; Pump\textsuperscript{18} reported the same. Glazier et al\textsuperscript{19} found 3.7 to 6.5 \( \mu \)m for zone III conditions in the rabbit. For zone III conditions, we found alveolar tubules of 5.8-\( \mu \)m diameter in the rat.\textsuperscript{11} Sobin et al,\textsuperscript{4} in the cat, found that \( h \) (capillary diameter in our paradigm) was 7.4 \( \mu \)m at 15 mm Hg distending pressure, suggesting a degree of overdistension compared with the average of 5.7 \( \mu \)m in the four cited reports (or, less likely, a marked species difference).

Corner Vessels

The phenomenon of corner vessels remaining partially open in zone I and II conditions due to the forces of intersecting alveolar walls\textsuperscript{19} is not consistent with the sheet-and-post theory, since posts would prevent collapse in zone I conditions throughout the alveolus, not just at the corners.

Are Biconcave Posts Simply Bioconvex Paired Capillary Walls?

If a single section from a tissue block is viewed in a certain way, the external walls of two adjacent tubules and the tissue space between them may appear to be a post. However, for the illusion to become convincing, all of the capillaries would have to be at the same distance apart in order that the posts would appear to have reasonably uniform diameters. This has not been demonstrated; the spacing of capillaries in our micrographs is random, which would produce posts that varied greatly in diameter. Unfortunately, the histology of the posts has not been defined.

The Literature Concerning Function

Rheology

Although Sobin et al\textsuperscript{1} rejected Poiseuille's law (Flow = \( [P_1 - P_2] \pi r^4/8 \mu L \), where \( P \) is pressure, \( r \) is the radius, \( L \) is the length of the tube, and \( \mu \) represents viscosity), their own formulation is quite similar. Note that both their formula for sheet flow and Poiseuille's law contain diameter (or radius) raised to the fourth power. In fact, Overholzer et al\textsuperscript{20} found similar fractions of the total resistance contributed by the microcirculation resistance when calculated by the two formulas (50 percent and 45 percent).

Recruitment and Distension

The sheet-and-post theory is not compatible with experimental data for three zones relating capillary pressure to alveolar pressure. Capillaries have been shown to be nearly collapsed in zone I,\textsuperscript{19} with diameters ranging from 2.0 to 2.8 \( \mu \)m; dimensions were 2.8 to 5.0 \( \mu \)m for zone II and 3.7 to 6.5 \( \mu \)m for zone III. Fung and Sobin's smallest \( h \) was 4.3 \( \mu \)m. The elegant morphologic studies of Assimacopoulos and coworkers\textsuperscript{21} clearly established that complete collapse of capillaries occurs in the presence of increased alveolar pressure; they concluded that the alveolar capillaries behaved more like plastic membranes than like elastic membranes, favoring the concept of recruitment over that of distension. There is no doubt that alveolar capillaries demonstrate recruitment; Hanson and colleagues\textsuperscript{22} measured a 165 percent increase in the number of capillaries with flow after large fluid infusions and a 96 percent increase with hypoxia.

The sheet-and-post model depends on distension rather than recruitment, whereas West et al\textsuperscript{23} regarded capillary distensibility as only marginal in importance.

Diffusion

Gas exchange would be optimized for the capillaries by concentrating the structural support between two layers of capillaries, away from the gas layer of the alveolus.\textsuperscript{14} In contrast, a single layer of sheets would
have to contain structural elements on the alveolar side of the microcirculation, interfering with diffusion.

Regardless of whether there is a single or a double layer, short tubules have a better surface-to-volume ratio for diffusion compared with sheets.

**Venous Flow Pulsatility**

Pulsatility of venous flow has been demonstrated to depend, in part, on transmission of the arterial pulse through the pulmonary capillaries and into the pulmonary veins. Sheets such as diagrammed by Fung and Sobin would produce more damping than capillaries, because their large middle segments and small inlet and outlet would produce a windkessel effect, and would be less likely to transmit the pulmonary artery pulse to the pulmonary veins.

**References**

10. Weibel ER. Morphometry of the human lung. Berlin: Springer-Verlag, 1963; 78