Why Doesn't the Elephant Have a Pleural Space?

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The elephant is the only mammal whose pleural space is obliterated by connective tissue. This has been known for 300 years but never explained. The elephant is also the only animal that can snorkel at depth. The resulting pressure differences require changes in the pleural membranes and pleural space.

In 1681, Mullen (8) dissected an elephant "accidentally burnt in Dublin on Fryday [*sic*], June 17" and reported that the pleurae "were so joyned that there was not one place where you might see a natural separation of them...contrary to what I ever observed in other Quadrupeds." Many other authors since then have found that the pleural cavity of the elephant is obliterated by connective tissue (for references, see Ref. 12), although it is interesting to note that the fetal elephant has a normal pleural space (4) that is obliterated late in gestation (9).

There has been no convincing explanation for this anatomic peculiarity, which is seen in both the African (*Loxodonta africana*) and Asian (*Elephas maximus*) species. It has been suggested that the obliteration protects the lung against spontaneous pneumothorax when the animal raises water through its trunk (9), but since the difference between alveolar pressure and intrapleural pressure is determined only by the elastic recoil of the lung, this difference would not be altered by this maneuver. Another suggestion is that absence of the pleural space helps to prevent distortion of the large lung by its weight (3), but the much larger lung of the blue whale (*Balaenoptera musculus*) has a normal pleural space. In addition, the loose connective tissue between the pleurae in the elephant is very extensible and presumably allows the lung to slide over the chest wall, so the support given to the lung is presumably limited (3).

Another unique feature of the elephant is its trunk, and this allows it to snorkel at depth, as observed by Aristotle (2) some 2,300 years ago: "Just then as divers are sometimes provided with instruments for respiration, through which they can draw air from above the water, and thus may remain for a long time under the sea, so also have elephants been furnished by nature with their lengthened nostril; and, whenever they have to traverse the water, they lift this up above the surface and breathing [*sic*] through it." There are many descriptions of elephants crossing rivers or lakes by walking on the bottom while breathing through the trunk, the tip of which just protrudes above the surface. As an example, Tennent (10) wrote "In crossing deep rivers, although his rotundity and buoyancy enable him to swim with a less immersion than other quadrupeds, he generally prefers to sink till no part of his huge body is visible except the tip of his trunk, through which he breathes...." Elephants are also strong swimmers (Fig. 1), and there are reports that they can swim for hours at a time while breathing through the trunk.

Many studies now suggest that the elephant has an aquatic ancestry (for references, see Ref. 5), and it is possible that the trunk evolved to enable it to snorkel while living in water, with obvious survival advantages. There is evidence that the elephant (order *Proboscidea*) and the sea cows (*Sirenia*) share a common ancestor. The evidence for this includes the development of nephrostomes (connections between the fetal kidney and the coelomic cavity), features of dentition, anatomy of the middle ear, and intra-abdominal location of the testes.

Physiological consequences of snorkeling

Snorkeling at depth creates very large pressure differences in the immediate vicinity of the lung. The reason for this is shown in Fig. 2*B*, which is drawn assuming that the bottom of the elephant lung is 2 m below the surface of the water. This is a reasonable assumption because the shoulder height of an African elephant can exceed 4 m. At this depth, the water pressure is ~150 mmHg, and this means that all of the vascular pressures are increased by the same amount. If this were not the case, no perfusion of the tissues with blood would be possible. However, the pressure in the alveoli is close to atmospheric because they are connected to the surface by a tube. Therefore, near the outer surface of the lung the pressure abruptly changes from 0 to ~150 mmHg. This is the basic dilemma faced by the pleural membranes.

The problem is highlighted by considering the small blood vessels in the parietal pleura. Figure 3 shows the histology of the parietal pleura from a typical mammal, in this case a sheep. Note that the pleural membrane is only ~30 μm thick and that it lies on the endothoracic fascia. There is a single layer of mesothelial cells, and the microvessels are very close to the pleural surface. The transudate from these microvessels enters lacunae and is then discharged into the pleural space, thus providing the fluid that lubricates the two pleural surfaces so that they can slide over each other.

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FIGURE 1. Elephants swimming in a lake near Chobe, Botswana while breathing through their trunks. Sometimes they allow themselves to sink and walk on the bottom so that only the tip of the trunk is visible. Photograph by R. Saxon.

It is easy to see that this anatomic arrangement would be impossible in the snorkeling elephant. The microvessels of the parietal pleura are supplied from the systemic circulation, in which the venous pressure exceeds 150 mmHg (Fig. 2*B*). Therefore, the pressure inside the pleural microvessels shown in Fig. 3 must exceed that. However, the pressure in the pleural space (if one exists) will be very close to alveolar pressure (that is, atmospheric), only differing from this by the elastic recoil of the lung. In other words, the microvessels of the parietal pleura will have a transmural pressure approaching 150 mmHg. Clearly, they would either rupture or the great imbalance of the Starling forces would rapidly cause massive transudation.

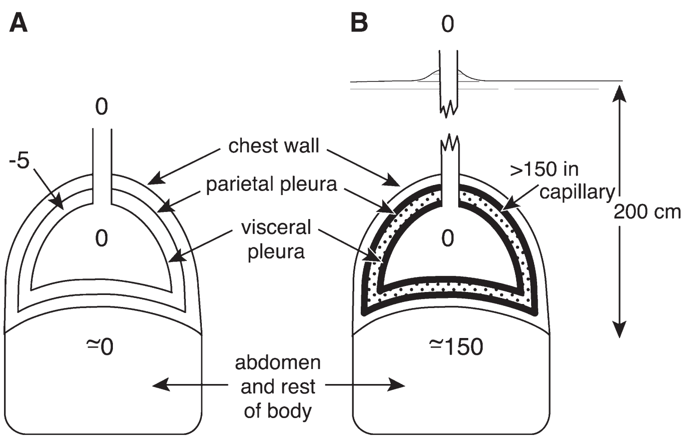

FIGURE 2. *A*: approximate distribution of pressures (in mmHg with respect to atmospheric pressure) in and around the lung for most terrestrial mammals. *B*: distribution of pressures in the snorkeling elephant. The bottom of the thorax is assumed to be 200 cm below the surface, and therefore the water pressure is ~150 mmHg. Systemic arterial and venous pressures will rise by the same amount, but the pressure in the alveoli is atmospheric (0). A microvessel in the parietal pleura has a pressure within it of >150 mmHg because it is supplied by systemic blood. If the anatomy were the same as shown in *A*, the transmural pressure of the microvessel would be >150 mmHg (compare Fig. 3). Evolution's answer is to replace the delicate pleura with dense connective tissue. The visceral pleura is also at risk and thickened. A layer of loose connective tissue, indicated by stippling, allows some sliding of the two pleural surfaces.

The microvessels of the visceral pleura may face a similar problem, although here the situation is more complicated. In large mammals such as the sheep, pig, horse, and human, the capillaries of the visceral pleura are supplied by the systemic bronchial circulation (1, 7). However, in smaller mammals such as dog, cat, and rabbit, the blood supply comes from the low-pressure pulmonary circulation. No direct anatomic information exists in the elephant, although because of its very large size the blood supply is presumably from the systemic circulation. In addition, the distance between the surface mesothelial cell layer and the underlying microvascular network is greater in the visceral than the parietal pleura (1), so this would make them less vulnerable.

Evolution's solution

As indicated above, the most vulnerable tissues during snorkel breathing at depth are those at the junction between the outside of the lung and the rest of the body, that is, the pleural membranes. Evolution has provided a remarkable solution to the problem by replacing the normally delicate parietal and visceral pleurae with sheets of dense connective tissue that prevent damage to the pleural blood vessels or excessive transudation. Figure 4 shows a photomicrograph of a portion of parietal pleura from an 18-yr-old male African elephant (3). Some intercostal muscle can be seen at the bottom of the micrograph, and above this is the parietal pleura, composed of dense connective tissue up to 500 μm thick in this example. Contrast this with Fig. 3, which shows the very delicate pari-

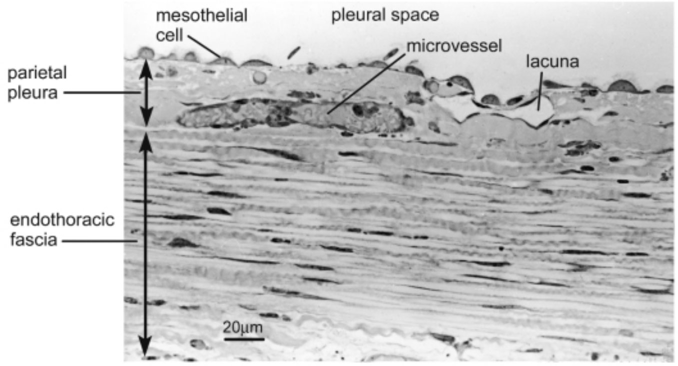

FIGURE 3. Photomicrograph of the parietal pleura and endothoracic fascia from a sheep. The parietal pleura is only ~30 µm thick. There is a single layer of mesothelial cells, and the microvessel is close to the pleural space and provides the transudate that traverses lacunae and lubricates the pleural surfaces. Courtesy of K. H. Albertine.

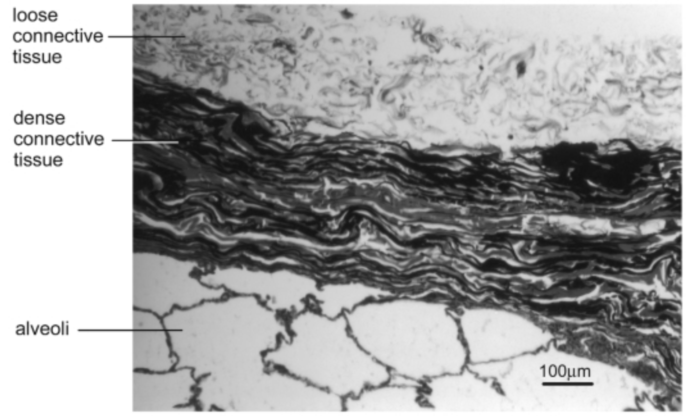

FIGURE 5. Visceral pleura from the same elephant as in Fig. 4. The layer of dense connective tissue has alveolar tissue below it and loose connective tissue above. Courtesy of R. E. Brown, J. P. Butler, and S. H. Loring.

etal pleura, only ~30 µm thick, from a sheep. There are no obvious vessels in the dense connective tissue layer shown in Fig. 4, but if there were any, they would be protected from rupture and edema formation, unlike the microvessels in Fig. 3, which are very near the pleural surface. Also note the layer of loose connective tissue in Fig. 4, which takes the place of the potential pleural space in other mammals and allows sliding to occur between the two pleural membranes.

Figure 5 shows a photomicrograph of the visceral pleura from the same animal (3). Alveolar tissue can be seen at the bottom of the section, and the layer of dense connective tissue is directly above that. In this instance, small blood vessels are apparently visible, but they will be protected from rupture or edema formation by the dense connective tissue encasing them. Again, loose connective tissue is seen above the dense connective tissue.

With this anatomic arrangement, the normal production of pleural fluid to lubricate the surfaces no longer exists. Recall that the pleural fluid normally comes from the microvessels in the parietal pleura, as shown in Fig. 3. However, as noted previously, the layer of loose connective tissue between the two dense connective tissue plates is very extensible, as emphasized long ago by Harrison (6) and more recently by Brown et al. (3). Therefore, some sliding of the two pleural surfaces across each other can occur. Having said this, the disadvantages of preventing sliding of the two pleural surfaces may not be very great. For example, humans who develop recurrent spontaneous pneumothorax are sometimes treated by inserting talc into the pleural cavity. This causes a low-grade inflammation that results in adhesion of the two pleural membranes (pleurodesis). The resulting interference with ventilatory function is small (11).

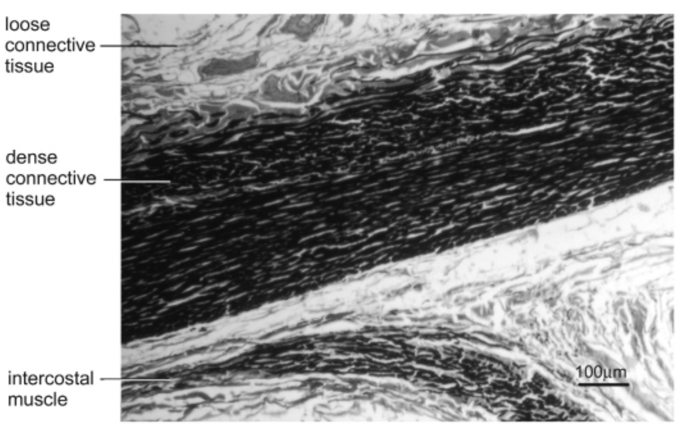

FIGURE 4. Parietal pleura from an African elephant (*Loxodonta africana*). The delicate pleural membrane shown in Fig. 3 has been replaced with a layer of dense connective tissue that overlies intercostal muscle. A layer of loose connective tissue is outside this. Courtesy of R. E. Brown, J. P. Butler, and S. H. Loring.

The hypothesis presented here is that the primary evolutionary response to the vulnerability of the pleural membranes is to replace these with plates of dense connective tissue. The obliteration of the pleural space by loose connective tissue, which is the most obvious anatomic peculiarity noted by Mullen (8) and many others, appears to be a secondary response brought about because the normal mechanism for providing lubricating fluid for the pleural membranes no longer exists, and there is apparently some advantage in allowing the membranes to slide over each other. The findings of Eales (4) in her study of the fetal African elephant support this hypothesis. She reported that the pleural cavities are "quite normal, but the mediastinal and diaphragmatic pleurae are greatly thickened." This is consistent with the assertion that the primary evolutionary change is thickening of the pleura to protect the microvessels, whereas the addition of a layer of loose connective tissue is a secondary response to allow sliding to take place. Incidentally, Eales stated that "the mediastinal and diaphragmatic pleurae are as much as 2 mm thick and are quite opaque." This is some four times thicker than the dense connective tissue plate shown in Fig. 4.

It is also interesting to note the mechanical problem facing the diaphragm during snorkeling. As Fig. 2*B* shows, the pressure difference across the diaphragm is ~150 mmHg, and this has to be sustained for many minutes while the animal is walking under the river or lake. This is a far greater transdiaphragmatic pressure than can be sustained by the human diaphragm. However, the elephant diaphragm is ~3 cm thick

(3), an order of magnitude thicker than the human diaphragm.

Finally, it should be pointed out that the relative pressure changes that occur when the elephant raises water in the trunk for drinking or washing are similar to those shown in Fig. 2*B*. In this instance, if the water is raised through 200 cm, the alveolar pressure must be 200 cmH_2O below atmospheric pressure, and the relative pressures are essentially identical to those shown in the figure. Since the elephant can raise water in its trunk with its mouth open (9), we know that the low pressure is not developed by the buccal muscles. It could be argued that this behavior, which is frequent in the elephant, is an additional evolutionary pressure for the anatomic changes in the pleural space. However, raising water in the trunk only takes a few seconds, whereas snorkeling lasts for many minutes and is therefore a much greater potential problem. As indicated earlier, the snorkeling behavior may have developed when the animal lived in water, and this would provide a very strong evolutionary pressure.

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