11 Separation of Respiratory Media in Gas Exchangers

The thickness of the tissue partitioning between water/air and blood in part sets the conductance, that is, the diffusing capacity (Do2) of a gas exchanger. Furthermore, Do2 is determined by factors such as the respiratory surface area, the volume of the pulmonary capillary blood, the prevailing partial pressure gradient and the permeability of the tissue compartments that O2 diffuses across (Fick’s law). The Do2 correlates directly with the surface area (S) and the permeation constants (K) and inversely with the thickness of the tissue barrier: Do2 = $S \cdot K/t$. In the vertebrate air breathers, the thickness of the blood-gas (tissue) barrier generally decreases from amphibian, reptilian, mammalian to avian lungs. Owing to the thick blood-gas/water (tissue) barrier, which measures between 20 and 50 μm, cutaneous gas exchange is characterized by limitations of diffusion (e.g. Malvin 1988). Increased vascularity (Fig. 115) and perfusion may promote O2 uptake, particularly during hypoxic episodes (e.g. Malvin and Hlastala 1986).

In fish gills, a thick water-blood barrier (Hughes and Morgan 1973) (Figs. 54, 55) and the presence of an unstirred boundary water layer over the secondary lamellae may curtail O2 transfer, producing significant diffusion limitations (e.g. Randall and Daxboeck 1984). Although generally thicker than the blood-gas (tissue) barrier of the lungs, the water-blood barrier in the gills of certain species of fish may be as thin as 0.2 μm in some parts (e.g. Hughes and Morgan 1973; Maina 1991). In mammals (e.g. Gehr et al. 1981) birds (e.g. Maina 1989b; Maina et al. 1989a) and even fish (e.g. Hughes and Morgan 1973), the thicknesses of the tissue barriers of the gas exchangers correlate with the metabolic needs as well as the environment in which they live. The tuna, *Katsuwonis pelamis*, one of the most energetic fish, has a water-blood barrier that is only 0.6 μm thick (e.g. Hughes and Morgan 1973), and *Oreochromis alcalicus grahami*, a fish that lives in the hot, highly alkaline Lake Magadi of Kenya that is virtually hypoxic at night, has a barrier that is as thin as 0.2 μm (e.g. Maina et al. 1996b).

The pathway that O2 traverses from the external environment to the tissue cells and ultimately into the mitochondria consists of a panoply of tissue components and spaces (Figs. 2, 54, 55, 97–99, 121) that differ in complexity and design. To promote the flux of the respiratory gases across a thin barrier, minimal tissue is located over the respiratory surface. In fish gills, for example, a thin secondary epithelium overlies the secondary lamellae (Figs. 54, 55), whereas the cellular elements such as the chloride (= mitochondria rich = ionocytes) cells and mucous cells are found in the composite...
primary epithelium that lines the gill filaments (Figs. 12, 51, 117, 119). The nonres­
piratory functions of the gills such as osmoregulation and ammonia excretion occur in
the primary epithelium, whereas gas exchange takes place strictly across the secon­
dary epithelium; an epithelial cell and its basement membranes, an interstitial space
and an endothelial cell with its basement membrane essentially constitute the water­
blood barrier (Figs. 54, 55). By locating most of the cellular and connective tissue
elements in the primary epithelium, the water-blood barrier becomes thinner. In fish
(Figs. 52–56, 107, 111) and crustacean (Figs. 66, 121) gills, endothelial cells are ar­
ranged as struts that span the space between the parallel, diametrically located ep­
ithelial cell sheets. While slowing down the flow of blood and hence promoting gas
exchange, the pillar cells render structural integrity to the secondary lamellae and gill
filaments of the fish and crustacean gills, respectively. They prevent overdistension
and mechanical damage of the vascular spaces under excessive intramural blood
pressures. In the gill filaments of *Potamon niloticus* (Maina 1990b), prolongations
of epithelial cells form sporadic zip-like pillar extensions (Fig. 121).

In the fish gills and the lungs of the lungfishes (Dipnoi), amphibians and reptiles
(e.g. Hughes and Weibel, 1976; Maina 1987a; Maina and Maloiy 1985, 1988; Perry et al.
1989), an interstitial space occurs between the basal cell membranes of the epithelial
and endothelial cells (Figs. 31, 55, 95, 128, 132, 134). The interstitial space may contain
nerves (Fig. 134), lymphatic vessels and connective tissue elements such as collagen,
elastic tissue and smooth muscle (Figs. 89, 90). In the blood–gas tissue barrier of the
avian lung, an interstitial space is, however, lacking (Figs. 97, 98): The basal cell
membranes of the epithelial and endothelial cells have fused into a common basement
membrane. This has contributed to the remarkably thin blood-gas (tissue) barrier
that characterizes the avian lung (e.g. Dubach 1981; Maina 1989b, 2000b, c; Maina et al.
1989a). In rare cases where air capillaries lie adjacent to each other (Figs. 58, 62, 126),
the basement membrane is lacking. This indicates that, developmentally, the formation
of the basement membrane is determined by the endothelial and not the epithelial
cell. In the avian lung, the endothelium constitutes 67%, the basal lamina 21% and the
epithelium 12% of the volume of the blood-gas (tissue) barrier (Maina and King
1982). The endothelial cells of the blood capillaries of the gas exchangers contain
numerous microginocytic vesicles (Figs. 89, 90, 95, 97, 98, 134), and those of the
avian lung are particularly highly sporadically attenuated (Figs. 97, 98, 126). The ratio
between the arithmetic mean thicknesses (tt) and the harmonic mean thicknesses
( tth) of the blood-gas (tissue) barrier indicates the degree and intensity of corruga­
tion of the blood-gas (tissue) barrier (e.g. Maina and King 1982). In the avian lung, the
mean of the minimum tth of the blood-gas (tissue) barrier is as small as 0.068 µm
(Maina and King 1982) and the mean ratio of tt to tth is 8:1. The sporadic attenuation
of the endothelium, whereby extremely thin areas are generated without risking the
mechanical integrity of the lung, appears to be a common scheme evoked in the
design of the gas exchangers of the higher vertebrates to maximize transfer of O₂
without compromising the mechanical integrity of the blood-gas (tissue) barrier.

Compared with non-flying mammals, bat lungs have relatively thin blood-gas
(tissue) barriers (Maina et al. 1982; Maina and King 1984; Maina et al. 1991). The
thinnest barrier ( tth) of 0.1204 µm has been found in the flying fox, *Phyllostomus hastatus* (Maina et al. 1991). In the lungs of mammals and birds, the thickness of the
blood-gas (tissue) barrier appears to have been optimized (e.g. Maina 1989b; Maina et
al. 1989a; Maina 2000b,c). Although mammals span an enormous range of body mass