

Skin Breathing in Amphibians

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Skin breathing, or cutaneous, gas exchange is an important route of respiration in many aquatic or semiaquatic vertebrates, and is particularly well developed in the amphibians. The skin of amphibians contains a unique vasculature that facilitates oxygen (O₂) uptake and carbon dioxide (CO₂) excretion. Cutaneous gas exchange can fulfill routinely 0% to 100% of O₂ uptake and 20% to 100% of CO₂ excretion (1). Amphibians pay a price for this: They require a relatively thin epidermis and, as a result, suffer from high rates of water loss. Thus, amphibians are, for the most part, tied to an aquatic or semiaquatic life. Furthermore, unlike lungs or gills, the skin lacks a dedicated ventilatory pump and, as such, has been thought to be a poorly regulated respiratory organ, with little scope for change. Research over the past couple of decades has revealed that amphibians may exhibit partial control over the cutaneous vasculature, and that such control is under both neural and possibly hormonal control. For the purposes of this chapter, most information will be taken from literature on ranid frogs (Order Anura), because the majority of research has been done on this group.

AMPHIBIAN CUTANEOUS CIRCULATION

Most amphibians possess a double circulation – the pulmonary and systemic – consisting of a right and left atrium and an undivided ventricle. A similar blood flow distribution pattern exists in reptiles and certain air-breathing fishes (2) (see Chapter 5). Primarily deoxygenated (deoxygenated systemic blood plus oxygenated blood from the skin are mixed) blood returns to the heart via the right atrium, whereas oxygenated blood from the lung only returns to the heart via the left atrium. Both atria connect to the single, undivided ventricle, although considerable flow separation of blood is achieved through the extensive system of trabeculae within the ventricle (3,4). Upon ventricular contraction, deoxygenated blood primarily travels through the spiral valve to the pulmocutaneous artery, which subsequently divides into the pulmonary and cutaneous artery. Oxygenated blood, on the other hand, travels via the aorta to supply blood to the tissues and other parts of

the skin. Thus, the skin generally receives blood from both the systemic and pulmocutaneous circuits (Figure 9.1). Specifically, at least in *Rana catesbeiana* (the American bullfrog), the dorsal skin receives blood primarily from the cutaneous artery, whereas skin surrounding the legs and, to some extent, the ventral surface receives mainly systemic blood (5). The skin circulation is drained by a pair of large cutaneous veins that feed into the subclavian veins and back to the heart. Thus, the skin receives both oxygenated and deoxygenated blood, but returns oxygenated blood to the heart, which is subsequently mixed with deoxygenated blood from the systemic circulation before returning to the right atrium.

A further aspect of import of the amphibian circulation concerns the innervation of the primary circulations to the lung and skin. The cutaneous artery is innervated by adrenergic fibers of sympathetic origin, which cause constriction. The pulmonary arteries themselves are innervated by cholinergic fibers of parasympathetic origin (i.e., the vagus) which cause constriction of the pulmonary artery and dilation of the cutaneous artery (6,7). This reciprocal autonomic innervation of the pulmonary and cutaneous arteries leads to situations in which blood can be directed to the respiratory organ that has the greatest potential for gas exchange. In most cases, this will be the lung, although in cases when the lung is hypoxic, hypercapnic, or poorly ventilated (e.g., during diving), blood flow to the lung will be decreased and blood flow to the skin will at least remain constant, if not increase (8,9).

CUTANEOUS VASCULATURE

In many amphibians, 20% to 95% of the entire body's respiratory capillaries are in the skin (Figure 9.2) (10). Indeed, in the smaller frogs, skin capillaries can be more abundant than pulmonary capillaries (10). In Czopek's examination of amphibian skin, he observed that the epidermis is only four to seven cell layers thick. Overall, the dorsal epidermis is 10% to 20% thinner (18–24 μm) than the ventral epidermis (32 μm). Unlike in most vertebrates, the skin capillaries are located inside the epidermis rather than the dermis, making

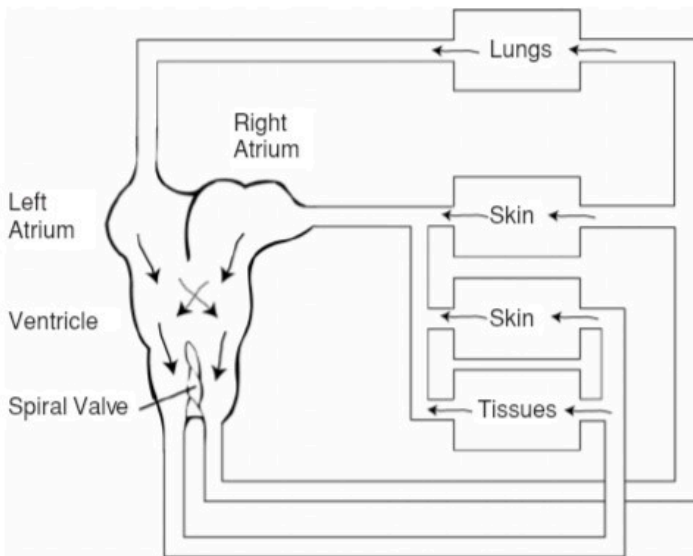


Figure 9.1. Schematic of the generalized circulation in amphibians. Arrows indicate the direction of blood flow. Dotted arrows indicate that a portion of blood can be shunted from one side of the heart to the other within the undivided ventricle.

the barrier to gas exchange much shorter (see Figure 9.2). The values quoted above, however, were from a rather unique amphibian. The epidermis of most frogs is two to three times thicker, although the respiratory capillaries still lie within the

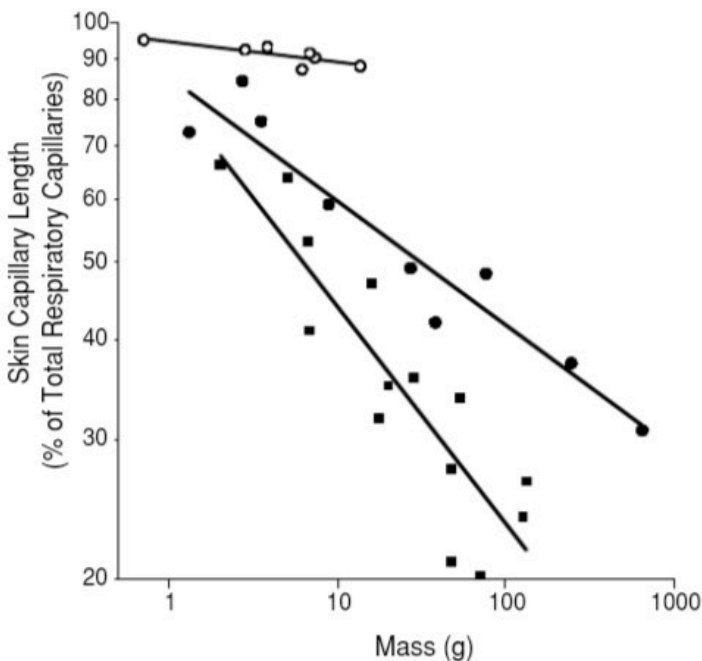


Figure 9.2. The percentage of respiratory capillaries that are cutaneous in origin differs among groups of amphibians. Lungless salamanders (open circles) have greater than 90% of respiratory capillaries in the skin, with the remainder found in the buccal cavity. Lunged salamanders (filled circles) and frogs (squares), on the other hand, have substantial respiratory capillaries in the lungs, buccal cavity, and skin. Note the trend with increasing body size for the skin to play a decreasing role in providing a vascular network for gas exchange. (Values adopted from Szarski H. The structure of respiratory organs in relation to body size in amphibia. *Evolution*. 1964;18:118–126.)

epidermis. This barrier for gas exchange (18–60 μm) exceeds that of lung epithelium by one to two orders of magnitude, making the diffusive transfer of gases a relatively slow process.

The respiratory capillaries form a vast network of anastomosing vessels (Figures 9.3 and 9.4) lying within the epidermis and forming a virtual sheet for gas exchange (11). These respiratory capillaries are connected to the skin arteries via branching arterioles, and they drain into subcutaneous veins via venules that penetrate the dermis. Very few true (i.e. systemic) capillaries connect the arterioles directly to venules or the venular network. Flow within the respiratory capillaries themselves exhibits a high degree of heterogeneity (12). Furthermore, the number of capillaries perfused can significantly affect gas exchange (13), although the nature of the regulation of these flows is unknown (i.e., whether it occurs at the arteriolar level or within the capillary network itself). Some clue to this may come from studies examining microvascular permeability (14). Although the respiratory capillaries themselves lack smooth muscles, microfilaments within endothelial cells (ECs) have been proposed to be part of a contractile machinery within the frog skin capillaries. These ECs within the capillaries alter their shape and appearance under electrical stimulation (14). Whether they operate in this manner in vivo, respond to neural or hormonal stimulation, or respond to changes in respiratory gases is unknown.

SKIN AS A GAS EXCHANGER: ROLE OF DIFFUSION

As in any respiratory organ, the diffusion of gases occurs across a layer of tissue and into the nearby bloodstream. Across large distances, the molecular movement of respiratory gases, which is governed by Fick's law of diffusion is not a very efficient process¹; therefore the larger the barrier between environmental concentrations of respiratory gases and the internal concentrations, the longer it takes for diffusion to occur. Some amphibians have anatomical modifications that capitalize on Fick's law of diffusion by increasing the total surface area available for gas exchange. The salamander, *Cryptobranchus* (15), and the Lake Titicaca Frog, *Telmatobius* (16), have marked folds in their skin that allow for greater diffusive exchange area, and these species are thought to make very little use of their lungs for gas exchange (15). In addition, the male hairy frog, *Astylosternus*, develops epidermal "hairs" during its breeding season that may supplement the total gas exchange surface (17).

Gas exchange across the skin of amphibians is believed to occur between the skin and an "infinite pool" of gases from the direct, surrounding environment (18). However, theoretical considerations and empirical evidence show that an external

1 Fick's law of diffusion: $= \frac{dQ_g}{dt} = D_g A \frac{dP_g}{dx}$ where $\frac{dQ_g}{dt}$ is the rate of diffusion of gas (g), D_g is the Krogh diffusion coefficient, A is the surface area, dP_g is the partial pressure gradient, and dx is the diffusion distance.

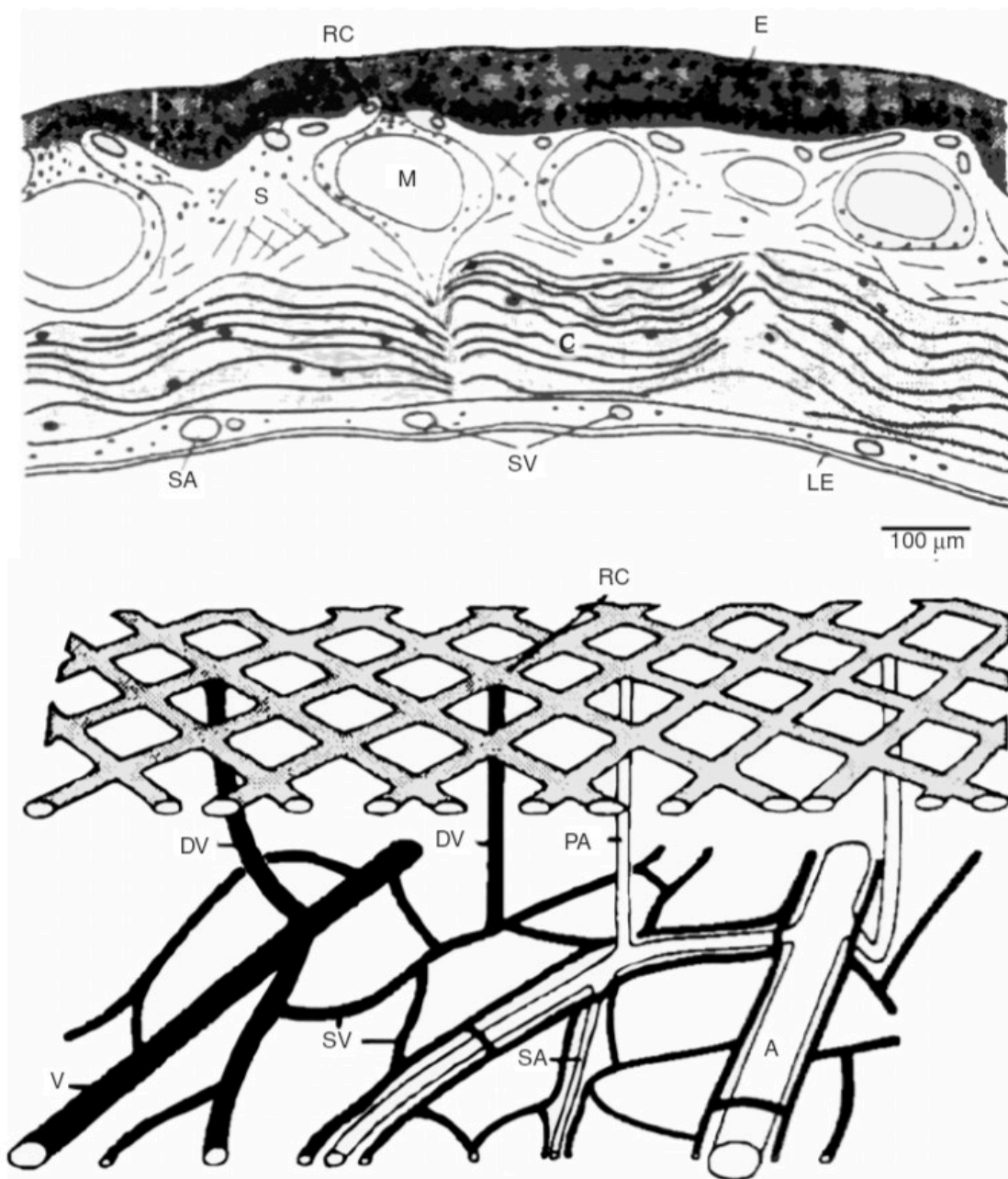


Figure 9.3. Organization of skin microcirculation in amphibians. *Top*: Cross-sectional schematic of frog skin, showing the relative placement of blood vessels within and beneath the epidermis. *Bottom*: Schematic of the network of blood vessels within the skin. Mucous gland (M), Stratum Compactum (C), Stratum Spongiosum (S), Skin arteries (A), branching arterioles (SA), subepidermal or respiratory capillary network (RC), arteriolar branches (PA), venules (DV), subcutaneous veins (V), subcutaneous venular plexus (SV), epidermis (E), lymph endothelium (LE). (Reproduced with permission from Olesen SP, De Saint-Aubain ML, Bundgaard M. Permeabilities of single arterioles and venules in the frog-skin – a functional and morphological-study. *Microvasc Res.* 1984;28:1–22.)