Reprinted from HANDBOOK OF PHYSIOLOGY – THE RESPIRATORY SYSTEM II
*Printed in U.S.A.*

93

CHAPTER 28

# Control of breathing in ectothermic vertebrates

GRAHAM SHELTON | *Department of Biological Sciences, University of East Anglia, Norwich, England*

DAVID R. JONES
WILLIAM K. MILSOM | *Department of Zoology, University of British Columbia, Vancouver, Canada*

CHAPTER CONTENTS



---

DESPITE THE TIGHTLY WOVEN THREAD of evolutionary change running through the six classes of the vertebrate subphylum with present-day representatives (cyclostomes, fishes, amphibians, reptiles, birds, and mammals), unifying principles applicable to physiological mechanisms are sometimes difficult to find. A wide diversity of habit among the vertebrates accounts for much of the physiological variety. Nowhere is this more obvious than in the case of breathing mechanisms and their associated control systems that relate breathing both to environment and to animals' needs. Attempts to produce general theories, e.g., of pH regulation (414, 434, 435), are more interesting than they are unifying, and other general treatments, e.g., of ventilation patterns (113, 117) or gas exchange (401), seem to emphasize differences rather than similarities in respiratory physiology.

The major modifications in respiratory systems during vertebrate evolution are unquestionably those associated with the change from breathing in water to breathing in air. The physical properties of the two media place totally different demands on the gas-exchange systems. Density, viscosity, and gas-diffusion characteristics have important effects on the evolutionary design of gas exchangers. These effects have been discussed by many authors, of whom Dejours (116) and Piiper (401) are among the more recent. The relative concentrations of respiratory gases that result from animals breathing in water or air are particularly significant in the evolution of adequate control systems. In water, low $O_2$ solubilities and hence low $O_2$ concentrations mean that aquatic animals must develop high ventilation and extraction rates to obtain the $O_2$ they need to live. In fact it seems that ventilation in fish is related primarily to their $O_2$ requirements. High $CO_2$ solubilities, however, lead to very low partial pressures of $CO_2$ ($P_{CO_2}$) in the gills, blood, and tissues of these animals (413), even when the degree of $O_2$ extraction from the ventilation stream is high. This is illustrated in Figure 1, in which the respiratory exchange ratio (R) line for water shows the possible combinations of partial pressures of $O_2$ ($P_{O_2}$) and $P_{CO_2}$ that can exist in the gills of an aquatic animal exchanging gases with a metabolic respiratory quotient (RQ) of 0.85. The low $P_{CO_2}$ values found in the blood of aquatic animals are accompanied by $[HCO_3^-]$ levels that by mammalian standards are equally low so that pH remains within physiological limits (241, 444). Regulation of $P_{CO_2}$ and pH in water-breathing animals can be achieved by ion-transporting mechanisms that are largely independent of ventilation (288), though some role for variations in ventilation, albeit a minor one, appears to exist. In air breathers, however, not only are the $P_{CO_2}$ and $[HCO_3^-]$