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Respiratory Pigments

Colored, metal-containing proteins that combine reversibly with oxygen, found in the body fluids or tissues of multicellular invertebrate animals and microorganisms. The role of these pigments is primarily to aid in the transport of molecular oxygen. Thus they are distinguished from respiratory enzymes, which are concerned with the metabolic consumption of oxygen. Four distinctly coloured groups of respiratory pigments exist among invertebrates: haemoglobins (purple, become orange-red with oxygen), chlorocruorins (green, become red with oxygen), hemocyanins (colorless, become blue with oxygen), and hemerythrins (colorless, become red with oxygen). Formerly, invertebrate haemoglobins were called erythrocruorins to distinguish them from functionally similar yet structurally distinct pigments of vertebrate bloods. Those hemoglobins confined to muscle cells are called myoglobins. A **respiratory pigment** is a molecule, such as haemoglobin in humans and other vertebrates that increases the oxygen-carrying capacity of the blood. The four most common invertebrate **respiratory pigments** are hemoglobin, hemocyanin, hemerythrin and chlorocruorin.

In the animal kingdom there are four types of O_2-binding (respiratory) pigment with different structures but very similar functional properties. They have characteristic colours in their oxygenated states and the absorption spectra of the pigments with bound O_2 or another ligand, such as CO or CN^-, are used for purposes of identification. The structures of the **binding sites** vary: the prosthetic group of the globins is protohaem, i.e. Fe(II)-protoporphyring, which can bind one ligand. Chlorocruorin is also a haemoprotein but with a haem component (spirographis haem) which differs from protohaem in one substituent. In the copper protein haemocyanin and the iron protein haemerythrin, the binding site in each case contains two metal atoms. Chlorocruorins and haemocyanins are always found dissolved in the blood plasma; haemerythrins occur only intracellularly, and haemoglobins are both intra-and extracellular. The intracellular respiratory pigments consistently have molecular masses under 100 kDA and only one to eight O_2-binding sites per molecule. Most of the extracellular blood pigments have far larger molecular masses of up to several million kDA and often more than 100 O_2-binding sites; in this way, the colloid osmotic effects in the blood plasma are reduced. There are, however, some exceptions to this rule, e.g. the extracellular haemoglobins of chironomid larvae are only 16–32 kDA.

Oxygen and carbon dioxide are transported in vertebrates and invertebrates by a wide range of respiratory pigments. These respiratory gases are not transported independently of one another, and this review considers the influence of carbon dioxide on oxygen transport and vice versa. A specific effect of carbon dioxide or bicarbonate, decreasing oxygen affinity, is found in many haemoglobins, but the effect is often reduced in the presence of organic phosphates. Clear experimental data are available for mammalian haemoglobins but in birds and lower vertebrates more data are required to verify the presence and magnitude of the CO2 effect. In erythrocruorins and haemocyanins CO2 increases O2 affinity, whereas in haemerythrins, as in haemoglobin, CO2 again decreases oxygen affinity. Much of our knowledge of invertebrate respiratory pigments is based, however, on data from one or two species. A specific effect of CO2 on O2 affinity has also often been found only at high CO2 partial pressures, which may be outside the physiological range for these species. More in vivo experimental data on CO2 values are required for these species, and further studies on other species may help to explain this discrepancy. The interaction of O2 and CO2 transport is mainly through the Haldane effect, i.e., deoxygenated blood having a greater capacity for CO2 than oxygenated blood. This is due directly to the formation of carbamino groups (carbamate) and also to the fact that deoxygenated blood binds relatively more protons than oxygenated blood. This forms the basis for the linkage between the Bohr and Haldane effects. In some species in which the Bohr coefficient is below −1.0, an akalosis in the tissues may be induced. Large Haldane effects may be particularly effective in promoting CO2 unloading when the partial pressure difference of CO2 between arterial and venous blood is small. Carbamate formation may account for 10–20% of the CO2 transported in mammals, but its role in lower vertebrates and invertebrates has only recently been considered. Carbon dioxide transport is modulated by those factors that influence O2 affinity as these in turn influence the Haldane effect.

Hemocyanin

The protein, called hemocyanin, is pale yellow when not combined with oxygen, and blue when combined with oxygen. The molecular weights of hemocyanins vary from 300,000 to 9,000,000. Each animal investigated thus far apparently has a species-specific hemocyanin.

Copper-containing proteins called hemocyanins occur notably in the blood of larger crustaceans and of gastropod and cephalopod mollusks. **Hemocyanin**s are colourless in the reduced, or deoxygenated, state and blue when exposed to air or to oxygen dissolved in the blood. **Hemocyanin**s serve as respiratory.

Hemocyanin, a copper-containing protein chemically unlike hemoglobin, is found in some crustaceans. **Hemocyanin** is blue in colour when oxygenated and colourless when oxygen is removed. Some annelids have the iron-containing green pigment chlorocruorin, others the iron-containing red pigment hemerythrin. In many invertebrates the respiratory pigments.

Hemerythrin

Hemerythrin is a non-heme iron protein used by two phyla of marine invertebrates (sipunculids and brachiopods) for oxygen transfer and/or storage. It differs from the other oxygen-binding proteins (hemoglobin and hemocyanin) both in the polypeptide chain and in the metal complex used to reversibly bind dioxygen. Haemerythrins form a class of non-haem di-iron O_2-binding proteins that display typical sequence and fold and are found only in invertebrates