Chapter 11

Respiratory Function of the Molluscan Hemocyanins

Ch. P. Mangum

Contents

1 Distribution and Phylogeny of the Molluscan Hemocyanins ................................. 301
2 Molecular Size and Structure .................................................................................. 303
3 Oxygen-Carrying Capacity of Molluscan Bloods .................................................. 305
4 Oxygen Equilibrium Properties of Molluscan Hemocyanins .................................. 307
  4.1 Polyplacophoran Hcs ......................................................................................... 310
  4.2 Gastropod Hcs .................................................................................................. 311
  4.3 Bivalve Hcs ...................................................................................................... 313
  4.4 Cephalopod Hcs ............................................................................................... 314
5 Physiological Functioning of the Molluscan Hcs ................................................... 315
  5.1 Polyplacophorans ............................................................................................. 315
  5.2 Gastropods ....................................................................................................... 316
  5.3 Cephalopods ..................................................................................................... 318
6 Summary and Conclusions ....................................................................................... 320
References ..................................................................................................................... 321

1 Distribution and Phylogeny of the Molluscan Hemocyanins

Hemocyanins (Hcs) are known in four of the eight (according to the scheme presented in a recent monograph; Table 1) classes of living mollusks: (Poly) Placophora, Gastropoda, Bivalvia, and Cephalopoda. Since the Solenogastres contain red blood cells (RBCs), it seems highly unlikely that they contain Hcs as well. The contents of the bloods of the Caudofoveata (chaetodermatids) and Monoplacophora are unknown. Information on this subject would be of considerable interest in understanding the evolution of the molluscan Hcs. N.B. Terwilliger (pers. comm.) carefully examined the blood of a scaphopod and found no spectrophotometric or electrophoretic evidence of a Hc.
The three subphyla in Table 1 group each of the classes known to contain a Hc with others either unknown or with RBC hemoglobins. Moreover, according to Fig. 1, the ancestral mollusk diverged first into the chaetodermatid and solenogaster-polyplacophoran lines, the latter diverging later to give rise to the other classes (Salvini-Plawen 1985). Thus, present knowledge permits either of the following evolutionary scenarios (or variants upon them): (1) The ancestral mollusk inherited from its vermiform ancestors a circulating body fluid complete with RBC Hbs, and Hcs arose shortly after divergence of the common ancestor of the remaining classes. (2) The ancestral mollusk invented both a circulatory system and an O₂ carrier, a Hc derived from an inherited tyrosinase (see Chap. 10, this Vol.); RBC Hbs arose independently, first in the Solenogastres and separately in the bivalves, in which the most primitive members retained Hc. According to the latter alternative, the total number of independent origins of the simple Hbs in the animal kingdom would increase to three. In my opinion, the first alternative is more consistent with the distribution of bloods and simple hemoglobins in animals (see Chap. 5, this Vol.), as well as the presence of heme proteins in the tissues of Hc-containing mollusks. In addition, the selection pressures for repeated replacement of Hcs by RBC Hbs are difficult to conceive (Mangum et al. 1987). The first alternative, however, is not the view favored by Salvini-Plawen (1985) and several other molluscan experts, who envisage an acoelomate turbellarian ancestor. This view is presently being eroded by analyses of RNA sequences, which support the more traditional relationship between the mollusks and the annelids (Field et al. 1988; Lake 1990). When sequence methodology, now in its infant stages, is further refined, the ultimate outcome will be of considerable interest.

In either case the basis of taxonomic separation of the polyplacophorans from the other Hc-containing classes is unclear (Fig. 1); the problem may arise from the way in which Salvini-Plawen's Fig. 42 was drawn.