This chapter deals with three interdependent systems. Pressurized filtration by the kidneys is affected by the affairs of the three hearts and these in turn by the movements of the mantle. Each is under nervous control and each must take into account the activities of the other two if it is to perform correctly. Research on the performance of the three systems has, however, usually been concerned with one system at a time and generally with one aspect of performance at a time. Sooner or later we shall have to try and monitor nerve impulses, pressure changes, oxygen and metabolite concentrations simultaneously, since these observations will undoubtedly reveal some very elegant control mechanisms. In the meantime, one is obliged to consider the workings of the three in the classical manner, one at a time; remembering that, eventually, the bits will patch together to yield a much more beautiful story.

The section that follows immediately deals with respiratory movements and their control. The main purpose of the movements is to oxygenate the blood and assist the escape of metabolites shed into the mantle cavity. The respiratory functions of the blood are dealt with below in Section 3.2.13; excretion, apart from the elimination of carbon dioxide which is considered in discussing the blood pigment, is reviewed in Section 3.3.

3.1 Respiration

3.1.1 Mantle movements

Like other molluscs, cephalopods have gills in a mantle cavity. Unlike the rest, the walls of the cavity are contractile. This immediately presents a problem because there is no hard skeleton for the muscles
to work against in expanding the respiratory chamber. The dibranchiate cephalopod solution to this difficulty has been the development of massive connective tissue lattices in the walls of the mantle, coupled with radial muscles in the thickness of the mantle wall.

Fig. 3.1 Diagrams showing structure of the squid mantle. (a) Diagram of *Loliguncula* mantle with skin and pen removed showing the thick muscle layer between outer and inner tunics. (b) Diagram of a longitudinal radial section of *Loliguncula* mantle to show relative thickness of the components in an animal with a mantle length of 120 mm. (c) Diagram showing the arrangement of muscle cells in the mantle of *Loliguncula*. Radial muscles, shown oriented vertically, attach to outer and inner tunics. (d) Diagram of the arrangement of large collagen fibres in the outer tunic of *Loliguncula*. Each of the seven layers is one fibre thick. Close packing of fibres in this array gives them rectangular cross-sections (from Ward and Wainwright, 1972).

The system has been worked out most thoroughly in squids. The main structural elements are shown in Fig. 3.1. There are circular and radial muscles and longitudinal lattices of collagenous fibres running helically around the mantle on either side of the muscle layer. In addition, and not shown in Fig. 3.1, there is a further longitudinal lattice in the plane of the radial muscles, between the inner and outer