Annelids occur in a variety of aquatic and terrestrial habitats. Most species, particularly among the polychaetes, are marine osmoconformers, in which the integument takes little or no part in creating an extracellular ionic milieu different from the ambient one. Integumentary permeability and transport processes may be involved, however, in other phenomena, including the passive changes and ensuing regulation of body volume under a fluctuating external salinity. A few species penetrate into brackish-waters, and in some of these the integument plays a decisive part in hyperosmotic regulation of the extracellular fluid. The same applies to those forms, notably among oligochaetes and leeches, which thrive in freshwater or water-logged soils. At least in certain cases, ion transport across the body surface appears to be linked to nitrogen excretion as well as to the regulation of the acid-base status of the internal fluids, and hence indirectly to respiration. Not only the exchange of inorganic materials, but also the transport of nutrients by the epidermis depends on the osmoregulatory state of the animal. Some annelids have adopted a terrestrial way of life and have acquired the ability to evade desiccation and to regain liquid water efficiently across the body surface to compensate for evaporative losses. With regard to

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respiration, soils and litters, the typical terrestrial habitats, normally maintain quite high oxygen and low carbon dioxide tensions, which lessens the problem of diffusive integumental gas exchange. Conditions are different in aquatic habitats, primarily due to the limited solubility of oxygen; in addition, many aquatic annelids live in sediments under extremely oxygen-poor conditions, and often with a high level of total carbon dioxide.

In the present chapter, the transport and permeability properties of the annelid integument in relation to respiratory gases, inorganic ions and organic compounds will be discussed in the light of the specific demands posed by the different habitats. It is emphasized that a comprehensive understanding of the integument as a barrier to and pathway of communication with the environment can be achieved only when a comparative study of the individual transfer processes is integrated into an analysis of their individual regulation and mutual interdependency.

20.2 Terminology and Basic Concepts

The term “permeability” is used in various meanings in the biological literature. Ideally, permeability (which physically has the dimension of velocity, e.g. cm s\(^{-1}\)) denotes the flux of a compound across a barrier of unit area resulting from a unit of driving force being applied across it; the driving force may be a difference in concentration, or more generally, in electrochemical potential of substrate between the two sides. This definition implies a linear relation between flux and force within a physiological range, and therefore use of the term (in the strict sense) is precluded whenever saturation phenomena are likely to be encountered. Furthermore, the rate-limiting barrier should be clearly identified and the driving force must relate to the inner and outer surface of this barrier (e.g. a particular cell membrane) rather than to distant points in the system; otherwise the electrochemical potential gradient may become partly dissipated in adventitious structures. In practice, these criteria are difficult to fulfill in complex biological systems such as invertebrate integuments, in which also the area of the rate-limiting barrier is often unknown or determined with little accuracy\(^1\). Therefore, the connotation of “integumental permeability”, as used in the literature, may range from being a vague indication of a material transport occurring more or less rapidly, to being a precise description of a physical property of some identified barrier within the integument. Since most solutes pass biological membranes by determined processes, “one only invites confusion to say that the membrane is permeable to (a) solute, i.e. that the solute freely permeates the membrane” (Christensen 1975).

The lipid matrix of cell membranes possesses a significant permeability (“ground permeability”) for a number of compounds, whether natural biologi-

\(^1\) To facilitate comparison between species, permeabilities will be given as cm s\(^{-1}\). The estimated epidermal area used for transforming original data will be stated for each case in the text. Intra-individual comparisons are not distorted by this procedure, since all values refer to the same area. However, the accuracy of inter-individual comparisons depend critically on the assigned surface area, and they should be taken to indicate order of magnitude only.