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Review

A structure–function analysis of ion transport in crustacean gills and excretory organs ☆

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Abstract

Osmotic and ionic regulation in the Crustacea is mostly accomplished by the multifunctional gills, together with the excretory organs. In addition to their role in gas exchange, the gills constitute organs of active, transepithelial, ion transport, an activity of major importance that underlies many essential physiological functions like osmoregulation, calcium homeostasis, ammonium excretion and extracellular pH regulation. This review focuses on structure–function relationships in crustacean gills and excretory effectors, from the organ to molecular levels of organization. We address the diversity of structural architectures encountered in different crustacean gill types, and in constituent cell types, before examining the physiological mechanisms of Na^+, Cl^-, Ca^{2+} and NH_4^+ transport, and of acid–base equivalents, based on findings obtained over the last two decades employing advanced techniques. The antennal and maxillary glands constitute the principal crustacean excretory organs, which have received less attention in functional studies. We examine the diversity present in antennal and maxillary gland architecture, highlighting the structural similarities between both organ types, and we analyze the functions ascribed to each glandular segment. Emphasis is given to volume and osmoregulatory functions, capacity to produce dilute urine in freshwater crustaceans, and the effect of acclimation salinity on urine volume and composition. The microanatomy and diversity of function ascribed to gills and excretory organs are appraised from an evolutionary perspective, and suggestions made as to future avenues of investigation that may elucidate evolutionary and adaptive trends underpinning the invasion and exploitation of novel habitats.

Keywords: Osmoregulation; Ion regulation; Gills; Antennal glands; Maxillary glands; Transport; Crustacean; Epithelia

Contents

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1. Introduction

Recent reviews of the physiology of crustacean osmoregulatory organs have usually and justifiably emphasized the gills, the principal organs responsible for homeostasis of the extracellular fluid in this diverse, mainly aquatic, arthropod group (Kirschner, 1979; Mantel and Farmer, 1983; Péqueux, 1995). However, crustacean excretory organs, variously known as antennal, antennary, maxillary, green or renal glands, have received far less attention, probably owing to their reduced size and more restricted accessibility. Consequently, while structural descriptions are common, comparatively less information is available on excretory function, and the identification and precise localization of membrane ion transporters and intracellular effectors is scanty, as are analyses of hormonal effects, also lacking for the gills. Further, the excretory organs have not been investigated electrophysiologically, a methodology which, as appreciated below, has furnished a wealth of knowledge on the nature of gill ion transport mechanisms.

Diverging from this trend, the antennal gland of the freshwater crayfish has been fairly well investigated, perhaps owing to its relatively large size. Riegel began micropuncture studies in the sixties (*e.g.*, Riegel, 1963, 1965, 1966a,b), leading to investigations in the nineties with membrane vesicle preparations aiming to localize and characterize transporters (*e.g.*, Ahearn and Franco, 1990, 1993; Behnke et al., 1990, 1998), and to recent molecular studies of calcium transporters (*e.g.*, Gao and Wheatly, 2004). Crustaceans possess various structures other than gills and excretory organs that perform osmoregulatory ion transport, such as the neck organ of the nauplii, and the metepipodites and gut of the brine shrimp, *Artemia salina* (Croghan, 1958; Conte et al., 1972), and the gut of terrestrial isopods (Wägele, 1992). These, and other extra-branchial and extra-renal sites of ion transport, are not within the scope of this review.

Interestingly, both these principal effectors of osmotic and ionic regulation, and of nitrogenous excretion, function cooperatively in terrestrial crustacean species. Modifications of the primary urine voided through the excretory pore by the branchial epithelium (Kobusch, 1994; Wolcott and Wolcott, 1985, 1991) will be dealt with in the section on the gills, and are mostly related to ion economy and the excretion of nitrogenous end-products (Wolcott and Wolcott, 1991; Kobusch, 1994). The elimination of nitrogen-containing compounds, another major function of excretory organs in general, is performed by both the gills and the excretory organs in the Crustacea, which are essentially, fully ammoniotelic arthropods. Even so, some crustacean groups have found alternative solutions for nitrogen excretion. For example, in isopods, nitrogen can be stored as urate in the 'Zenker's cells' (Walter and Wägele, 1990; Wägele, 1992). Terrestrial crabs like the robber crab *Birgus latro* perform fecal uric acid excretion (Greenaway and Morris, 1989), and in the terrestrial isopod *Porcellio scaber*, gaseous ammonia is intermittently volatilized from the pleon fluid, some ammonia also being converted and stored in the hemolymph and tissues as glutamate and glutamine (Wright and O'Donnell, 1993). This multiplicity of structures and solutions to similar functional challenges reflects the diversity of the Crustacea, which occupy marine, estuarine, freshwater, amphibious, semi-terrestrial and fully terrestrial habitats, and vary greatly in size and body plan. Where possible, in this review, the structure of the gills and the excretory organs will be related to the species' habitat or to acclimation salinity, and thus to the osmotic and ionic challenges encountered.

2. Gills

2.1. Gill structure

Crustacean gills constitute the amplified surface of a differentially permeable interface employed for ion and gas exchange between the internal and external media. The number of paired gills varies widely among the different taxa, and forms the basis for the so-called branchial formula. Depending on the location of gill attachment, pleurobranchs, arthrobranchs and podobranchs can be distinguished. A thin cuticle covers all gill