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A pancreatic exocrine-like cell regulatory circuit operating in the upper stomach of the sea urchin *Strongylocentrotus purpuratus* larva

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Abstract

Background: Digestive cells are present in all metazoans and provide the energy necessary for the whole organism. Pancreatic exocrine cells are a unique vertebrate cell type involved in extracellular digestion of a wide range of nutrients. Although the organization and regulation of this cell type is intensively studied in vertebrates, its evolutionary history is still unknown. In order to understand which are the elements that define the pancreatic exocrine phenotype, we have analyzed the expression of genes that contribute to specification and function of this cell-type in an early branching deuterostome, the sea urchin *Strongylocentrotus purpuratus*.

Results: We defined the spatial and temporal expression of sea urchin orthologs of pancreatic exocrine genes and described a unique population of cells clustered in the upper stomach of the sea urchin embryo where exocrine markers are co-expressed. We used a combination of perturbation analysis, drug and feeding experiments and found that in these cells of the sea urchin embryo gene expression and gene regulatory interactions resemble that of bona fide pancreatic exocrine cells. We show that the sea urchin *Ptf1a*, a key transcriptional activator of digestive enzymes in pancreatic exocrine cells, can substitute for its vertebrate ortholog in activating downstream genes.

Conclusions: Collectively, our study is the first to show with molecular tools that defining features of a vertebrate cell-type, the pancreatic exocrine cell, are shared by a non-vertebrate deuterostome. Our results indicate that the functional cell-type unit of the vertebrate pancreas may evolutionarily predate the emergence of the pancreas as a discrete organ. From an evolutionary perspective, these results encourage to further explore the homologs of other vertebrate cell-types in traditional or newly emerging deuterostome systems.

Keywords: *Strongylocentrotus purpuratus*, Pancreas, *Ptf1a*, Carboxypeptidase, Pancreatic lipase, Amylase

Background

The ability of a species to survive in a new environment is strictly related to its capacity to successfully digest and assimilate different food sources. A characteristic that is shared by all the living forms is the ability to digest large molecules available in their habitat to produce energy. Digestion relies on the function of enzymes that are able to break down proteins, lipids and sugars in the diet. The number of specialized enzyme-producing cell types

involved in food digestion increases with the complexity of the animal body and the variety of the meal. Metazoans typically have specialized exocrine cell types for the secretion of digestive enzymes. For example, gland cells that produce and release zymogens in the gastric cavity are scattered along the hydra gastroepidermis [1, 2] and along the digestive filaments of corals [3]. Cells rich in granular inclusions involved in extracellular digestion are localized along the foregut and in the gut caeca of different species of flat worms [4–6]. In different regions of the *Drosophila* midgut there are enterocytes that secrete a vast array of digestive enzymes, with expression levels matching organismal requirements [7]. A specialized organ geared toward

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