Subcellular Processes in Plants and Animal Cells

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Stem cells and progenitor cells in decapod crustaceans: diversity, cytological peculiarities and dynamics

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The philosophy in a scientific discipline is much dependent on the features of the research models used. In stem cell research, the best investigated systems come from vertebrates, mainly man, mouse and medaka. Exploitation of their specific features laid the foundation of modern stem cell biology. However, there are some interesting stem cell systems in sponges, cnidarians, flatworms, *Drosophila melanogaster* and *Caenorhabditis elegans* that have come into the focus of stem cell researchers in the last decade (references in [1]). Sponges and cnidarians have the advantage of simple body plans, flatworms are the masters of regeneration and the fly and nematode are genetically particularly well characterized. Indeterminately growing free-lancing invertebrates that can reach large body sizes and ages of decades have been neglected so far. The decapod crustaceans could fill this gap because they possess a remarkable diversity of embryonic and adult stem cells. The latter operate with high fidelity until old age resulting in the scarcity of age-related diseases and cancer in these animals [2, 3].

The Decapoda are conspicuous and abundant marine and freshwater invertebrates comprising some 14,760 species and dating back to the late Devonian (~360 million years ago). They include the commercially valuable shrimps, lobsters, crayfish and crabs and are keystone species in numerous aquatic habitats. Reliably determined life spans reach from 40 days to 72 years [2]. Due to their ecological and economical importance and traditional use as experimental animals they are amongst the best investigated invertebrates. Nevertheless, research on their stem cells is still at its infancy.

There are several well identified embryonic stem cells, among them the ectoteloblasts and mesoteloblasts that give rise to the ectoderm and mesoderm of the successively emerging thoracic and pleonal segments [4]. These stem cells form a highly ordered structure in the caudal papilla of the developing embryo that is composed of a superficial ring of 19 ectoteloblasts and a subjacent ring of 8 mesoteloblasts. The ecto- and mesoteloblasts remain active until completion of all body segments at the end of embryonic or larval development. Particularly interesting adult stem cells are the E-cells of the hepatopancreas, the satellite cells of the heart and skeletal musculature, the neurogenic stem cells of the brain, the stem and progenitor cells of the haematopoietic tissue and the germline stem cells.

The hepatopancreas is the most voluminous organ of the digestive tract and includes intestinal, hepatic and pancreatic functions. It is composed of hundreds of blindly ending tubules, which fuse together to form collecting ducts that finally terminate in the stomach. The hepatopancreatic stem cells, the so-called E-cells, are confined to stem cell niches located at the blind ends of the tubules (Figure 1A). These stem cells give rise to three mature cell types, the nutrient absorbing R-cells, the digestive enzyme synthesizing F-cells and the functionally obscure B-cells. Propagation of their descendants in one direction only produces a distinct age gradient along the tubules. E-cells divide in a late phase of the digestive cycle to replace discharged epithelial cells and are apparently regulated by a feeding-related signal. Consequently, they are virtually inactive during starvation.

In contrast to mammals, there are plenty of stem cells in the heart of decapods, the so-called satellite cells. These cells are small and spindle-shaped and scattered throughout the muscularis layer of the heart. Usually, they are adjoined individually to the muscle fibres (Figure 1B). Satellite cells are quiescent during intermoult and become active after ecdysis for a short period of time. Their descendants are integrated into the existing muscle fibre network in order to enlarge the heart after moulting. The activity of the satellite cells is regulated by the moulting hormone 20-hydroxyecdysone.

Decapods show a continuous production of new neurons in several parts of the brain, particularly in the olfactory deutocerebrum [5]. Each hemi-deutocerebrum includes a neurogenic system consisting of one neurogenic niche, two migratory streams and lateral and medial proliferation areas (Figure 1C). Progenitor cells are produced in the neurogenic niche from stem cells and migrate then to the proliferation areas where they divide and differentiate into various types of neurons, resembling closely the situation in higher vertebrates. In crayfish, the persistence of such new neurons depends very much on the social status of the animal, being higher in dominants than in subordinates [5].

The haematopoietic tissue contains stem and progenitor cells (Figure 1D), which give rise to three mature types of haemocytes, the hyaline cells, granular cells and semigranular cells. These blood cells have different functions in wound healing and immune defence. Decapods can autotomize and regenerate their limbs in response to injury or mechanical forces exerted by a predator's grip. Regenerated are the chelipeds, walking legs and antennae but not the eyestalks. Autotomy is a reflex and occurs at a pre-formed fracture plane. Regeneration of a lost limb is initiated by formation of a blastema that is produced by mitotically active cells in the epidermis and undifferentiated cells immigrating in large quantities along the pedal nerve. The latter are probably dedifferentiated cells from various sources [8]. The regenerative blastema produces different types of tissue such as musculature, connective tissue, epidermis, nervous tissue and sense organs.

The various types of stem cells in the Decapoda show quite different activity patterns. Some of them are continuously active for weeks such as the ectoteloblasts and progenitor cells of the regenerative blastema or for a lifetime such as the neurogenic stem cells. Others are cyclically activated and silenced in periods of a day such as the hepatopancreatic E-cells, weeks and months such as the satellite cells of the heart and skeletal musculature or months and years such as the germ cells. Proliferation is triggered by signals related to feeding, moulting or reproduction, respectively.

The biggest treasure that could be raised by stem cell research in the Decapoda concerns the regulatory mechanisms that guarantee error-free division of stem cells until high age, largely preventing age-related diseases and tumours in this taxon [2, 3]. Of course, it is presently not foreseeable whether uncovering of such mechanisms is exploitable for medicine but there is hope that research in this direction might evoke new ideas for the development of anti-ageing and anti-cancer interventions in humans.

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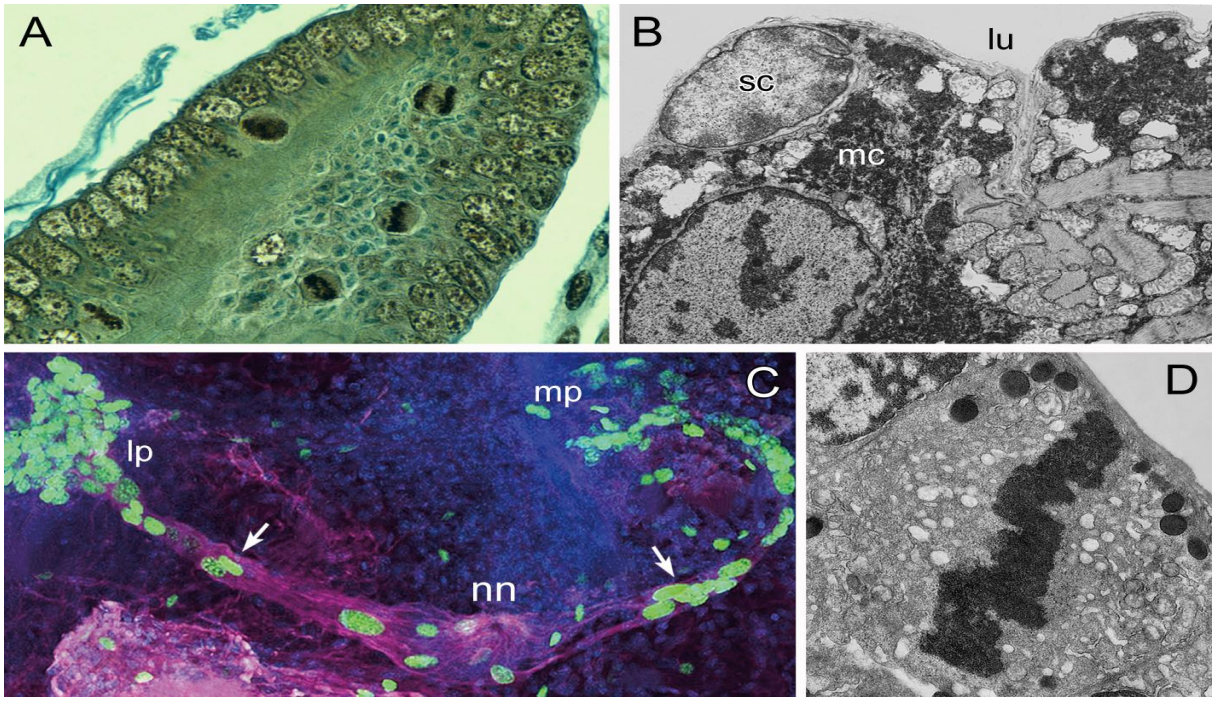

Figure 1 Adult stem and progenitor cells in decapod crustaceans. a) E-cell zone at blind end of hepatopancreas tubule of marbled crayfish with mitotic stages [3]. b) Satellite cell (sc) located between large myocardium cell (mc) and heart lumen (lu) in marbled crayfish [6]. c) Neurogenic system in hemi-deutocerebrum of red swamp crayfish showing migration of newborn cells (arrows) from neurogenic niche (nn) to lateral (lp) and medial (mp) proliferation areas [5]. d) Mitotic stage of progenitor cell of semigranulocyte in haematopoietic tissue of lobster [7].