

What triggered multicellular systems?

543 million years ago the fossil record shows divergence of macroscopic calcified animals, and over the next 20 million years or so, most of the basic body plans of animals recorded ever since evolved. This so-called Cambrian explosion has been used to argue for some sort of extraordinary, even non-Darwinian, underlying cause.

Although this issue is an unresolved puzzle, an evolutionary explanation is by no means impossible. Below, a feasible scenario based on Darwinian accumulation of small changes is outlined.

Why should a unicellular organism, like a bacterium, evolve into a multicellular species, which after investing in making lots of differentiated cells, use only a small fraction of these to make offspring? The unicellular bacterium is perfectly capable to divide itself to make offspring and at least 1500 million years of such successful cells predate multicellular systems.

However there is a number of Protozoan antecedents to multicellular functions:

- cellular adhesion used for recognizing and capturing prey.
- ability to monitor and respond to cues from environment and prey.
- protozoans capable of differentiation, but *temporally* rather than spatially. Signalling between cell types by pheromones or membrane-bound receptors make proper sorting of cells possible.
- stable cell adhesion permits exchange of genetic material.

Single cells may use microtubuli, either to form spindles inside the cell necessary during the process of cell division, or to form protruding flagella usefull for locomotion. It is known, however, that many so-called unicellular cells during their life cycles come together to form colonies. They may switch from dividing cells to so-called swarmer cells, which use their microtubules to migrate to presumptive better locations, and then switch back to dividing cells.

Genes for cell adhesion and signal transduction arose hundred of millions of years before the emergence of truly differentiated cell colonies. Approx. 800 million years ago (Mya) (uni-cellular) choanoflagellates (ancestors to animals) and by 750 Mya green algae (ancestors to green plants) and sponges had such genes. Genes for differentiation were well developed by the time that plants, fungi and sponges emerged, before or approx. 750 Mya. Also advanced gene regulation processes had emerged.

Some cells may engulfe other cells (phagocytosis) and eat them. The origin of this kind of predation have given evolutionary pressure towards growing size and uni-cellular systems are known which answer with colony formation in response to predator arrival. Cells in the division mode may not have microtubuli ready for locomotion, and a division of labor within a colony of cells with some cells doing the locomotion, others the cell divisions may have been at the origin of multicellular animal systems. Sponges (which may have originated about 750 Mya) have this kind of organization, and the cells with microtubuli display coordinated movements to transfer water (with organic material, ie food) to the rest of the colony. This kind of multicellular systems persisted for over 100 My at the sea bottom, without disturbing the mats of unicellular systems, which had existed for over 1000 My.

During the widespread recurring ice ages ending this period, life at the bottom of the sea came under severe stress. Sponge larvae, however, are not confined to the bottom, but search the water column for food. This may have triggered the process of gastrulation: on the outside cells with flagella doing the locomotion of the colony, in the inside of a hollow ball a layer of by now *differentiated* cells doing cell division.

Gastrulation (often arising from a hollow ball of cells, which invaginates to form a ball with an opening in one end) also gives rise to a very primitive mouth of size sufficient to swallow much larger prey than single cells could do. This would give even more pressure on prey to evolve into larger systems: size matters.

Indeed, so-called Ediacran fossils are known, some more than 600 My old f. ex. centimeter-scale radial symmetric species, but several body plans represented. Also fossils with repeated tube-like units, perhaps due to periodic growth. These fossils may perhaps represent the 'dinosaurs' which placed ecological constraints on the evolution of animals as we now know them (bilaterian body plans). Small bilaterian fossils (one tenth of a millimeter) 40-55 My before cambrian explosion 543 Mya have been found in China recently (2004).

The balance between species may have been upset and reversed after major ecological upheaval which affected uni-cellular cells, sponges and bilaterians alike: 3 or more major ice ages covering large parts of Earth, and one of the largest recorded impacts from space (Acraman impact) 580 Mya. Thus dramatic changes in ocean circulation occurred.

Cnidarians (Sea-anemones, hydra) are the most simple organisms to have neuromuscular system for movement (feeding). Porifera (sponges) by contrast have passive filtration. The Cnidarian nervous system has strikingly evolutionary conserved properties, and the nervous system may have originated only once. Origin may be linked to so-called Nematocytes. They are mechanoreceptor cells that contact prey and discharge poison to immobilize prey. Coexpression of identical regulatory genes suggest that neuronal and nematocyte pathways developed from common ancestral origin. Such mechanoreceptor cells (also in inner ear of vertebrates) perhaps the original, which evolved into neurons:

- First single cell autonomous reaction to prey.
- Then connections to neighboring cells, coordinated response.
- Then nerve net with resulting active feeding behaviour at one pole of animal. With time a more and more complex head may have evolved.

Thus ancestral neuro-epithelial cells preceded the establishment of organizer and patterning activity in animals, but many genes involved in the nervous system have been coopted for use in pattern generation in embryos.

The emergence of many body plans over a time span of 20 My may be linked to the emergence of the process of segmentation, although this view still is controversial. The essence of this mechanism is axial growth coupled to oscillating gene expression. This is a very simple mechanism, which may have played the role of a scaffold, upon which many refinements have been build subsequently. Replacement of ciliary locomotion with nerve/muscle-driven locomotion may have triggered important selective advantage.

The above shows that a route from uni-cellular bacteria to multicellular organisms with segmented embryos may have occurred with small steps, and thus the Cambrian Explosion could in principle be compatible with Darwinian evolution. The actual details in the above scenario is still a matter of much debate, but this is not the fundamental issue.

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