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Morphogenetic gradients in graptolites and bryozoans

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Despite independent evolution of coloniality in hemichordates and bryozoans, their colonies show common features. In both instances colony is a genet or clonal system composed of zygotic oozooid and a number of blastozooids (= modules) integrated by physical continuity of tissues, sharing a common genotype and subject to common morphogenetic control. In some groups of graptolites and bryozoans, colonies display a regular morphological gradient. Simple graptoloid and bryozoan colonies consist of a proximal zone of astogenetic change and a distal zone of astogenetic repetition. Observed morphological gradient may be attributed to diffusion, along the colony axis, of a morphogen produced by the oozooid; in the zone of astogenetic change the morphogen is above certain threshold level and drops below it in the zone of astogenetic repetition. This model is supported by observations on regeneration of fractured graptoloid colonies. Regenerative branch never displays astogenetic change. The same rule is valid for regeneration of fractured bryozoan colonies. While the early astogeny of simple bryozoan colonies may be explained within the framework of the gradient theory, the late astogeny of more complex ones involves multiple succession of zones of change and repetition, without analogy in astogeny of graptoloids. Thus, late astogeny in bryozoan colonies may be controlled by cyclic somatic/reproductive changes, probably independent of the primary morphogen. Evolutionary changes in the graptoloid colonies involve both the spreading of the novelties over a greater number of zooids (penetrance) and an increase in the degree of phenotypic manifestation of a given character (expressivity). In the phylogeny of bilaterian colonies morphogenetic gradient probably originated as a sort of a side effect of sexual process leading to the appearance of the oozooid. The latter contaminated the neighbouring blastozooids with the products of its own morphogenesis. The resulting morphogenetic gradient could be used by selective forces to produce various effects of adaptive significance. Morphogens responsible for patterning of bilaterian colonies are probably related to the products of genes responsible for the anteroposterior control of embryos in all solitary Bilateria (Hox, zootype genes).

Key words: Bilateria, graptolites, bryozoans, colonies, clones, morphogen, Hox genes.

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