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SOME REMARKS ON COLONY ORGANIZATION IN GRAPTOLITES

Abstract. — Implications of the presence of perithecal membrane for understanding the degree of integration of graptoloid colonies is discussed. In contrast to Kirk's (1975) opinion that graptoloid colonies can be thought of as a kind of super-individual, a view is advanced that most of morphogenetic functions were delegated to particular zooids. The share of common colonial structures is too small to consider graptoloid colonies as single individuals. Irregular and localized secretion speaks against the concept of rhabdosome being a precisely controlled counting device.

Recent ultrastructural studies may shed a new light on the organization of the entire graptolite colony especially when we accept the "membrane model" of the secretion of the periderm as defined before (Urbanek 1978: 595—629, in this volume). The presence of *perithecal membrane* — a sort all-enveloping soft tissue covering — and *stolonial system* made of graptolite colony an integrated unit. In my hypothesis concerning the organization of graptoloid colonies I presumed (Urbanek 1960, 1963, 1966, 1970) that their polar organization, peculiar morphogenesis involving a regular succession of thecae, and effects observed in regenerated rhabdosomes, may be explained by a sort of *physiological gradient*. This was attributed to elaboration by the siculozoid of a certain morphogenetic substance which later spread or diffuse to permeate the entire colony. This diffusion of morphogenetic substances between the zooids may have been effected by the stolon and extrathecal membranes spread among zooids as suggested by Kozłowski (1949). As the presence of extrathecal membranes was in my opinion at that time rather hypothetical than safely established, I put more emphasis on stolon as the way of spreading of morphogenetic substances, although extrathecal membrane has been also taken into considerations.

This is a starting point of criticism by Kirk (1975), who is convinced that continuous covering of soft tissues enveloping the colony („mantle" in her terminology) was instrumental both in secretion and in gradual changes of secretory epithelium responsible for astogenetic succession of

thecae. Up to this point I would gladly accept the view of Kirk, perhaps with an additional remark that this new opinion on the possible role of extra- (peri-) thecal tissues is largely due to the ultrastructural data supplied by Urbanek and Towe (1974, 1975), and which were unknown for me in 1970.

Dr. Kirk however, has also formulated and skillfully advocated an entirely new approach to the problem of graptolite coloniality. In her opinion problem of organization and morphogenesis of a graptolite colony is similar to that within a single metazoan individual. Graptolite colonies "can be thought of as manymouthed, super-individuals" (Kirk 1975: 19). Since the secretion by the epithelium was incremental, producing growth bands probably simultaneously over the whole rhabdosome, Dr. Kirk suggests that graptolite colony "constituted some kind of counting device giving precision response to biochemical changes occurring with time" (*op.cit.*: 18). In other words, development of graptoloid colonies "can be described in terms of incremental secretion in an internal environment gradually changing with time" (*op.cit.*: 19).

Except for emphasis on increment counting and their precise control Dr. Kirk's views appeal to a well known idea of a graptolite colony being essentially an individual due to high integration of zooids. When discussing this point of view (Urbanek 1960, 1966, 1970) I always suggested it is too simplistic. It seems inadequate to explain certain facts (e.g. introduction of phylogenetic novelties, Urbanek 1960), and does not agree with generally high degree of elaboration of thecae and their frequent isolation (instead of their embedding in common colonial tissue). Even in highly specialized graptoloids the share of common colonial structures was too low to consider them as colonial animals with most of morphogenetic functions delegated to a sort of caenosarc and controlled like one single individual. The growth of rhabdosome is realized through formation of a number of individual morphogenetic fields and most changes seems to be subordinated to control within such fields. Graptolite rhabdosome is still a construction composed of separate zooidal lodgings. Astogeny of graptolite colony, including graptoloids was due to budding of zooids with considerable autonomy. I would suggest that we cannot deprive graptolites their colonial nature, a dualistic state of biological organization, combining individual and superindividual aspects.

If we accept point of view suggested by Dr. Kirk that in the nature of facts a graptoloid colony is nothing but individual, her gradual biochemical changes occurring with time within internal environment of colony are reduced to trivial processes of aging. There is little reason, however, to accept this point of view as only a few known graptolites show any traces of senile changes and generally their colonies may be considered as systems open in time—a feature remarkably different from cessation of growth in solitary animals.

I would like to argue that we perhaps should avoid *ad hoc* hypothesis, created just to explain organization of graptolite colonies as a unique or a peculiar case, without paying enough attention to comparison with the coloniality in other animal phyla.

A remarkable feature of majority of colonial coelenterates and bryozoans is the presence of physiological gradients. It is clearly established that physiological gradients exist in majority of colonial invertebrates and express themselves in distribution of zooids, in more or less regular changes of morphogenetic potential power of growth and regeneration and in morphophysiological polarity. Hypothesis of physiological gradients is therefore based on solid background of comparative physiology and morphogenesis and by no means was it invented only to explain fact observed in one fossil group of animals. Theory of morphophysiological gradients which operates with terms of inhibition and regulation of growth has in my opinion a greater explanatory power as compared with ideas suggested recently by Dr. Kirk (Kirk 1975). Dr. Kirk offers nothing more than a certain truism — namely that everything what happens during astogeny is a co-ordinated realization of a genetic instruction innate to the colony. It does not explain how this potential is distributed between growing zooids and branches (cladia) of the colony — why some thecae are hooked and some straight and why the budding of some branches is inhibited. The only answer may be — I presume — that this is because of the specific content of the genetic instruction of a given colony. The generality of the concept I would say was achieved by the sacrifice of its meaningfulness. The concept of a graptolite colony, being some kind of an incremental counting device is doubtlessly an interesting idea, but it is nevertheless only a further development of previous ideas on the concomitant growth of multiramous rhabdosomes, which were elaborated along the line of morphophysiological gradient theory of graptolite organization. Simultaneous growth of multibrachiate rhabdosomes implies the same growth rate at growing tips, budding of new thecae step by step and may be therefore extrapolated over the simultaneous addition of increments (growth bands, layers). I can only be sceptical whether the control of morphogenesis was so rigid and precise as to allow to consider the approximately simultaneous addition of fuselli the main feature of graptolite colonies organization.

Irregular secretion of microfusellar tissue, localized secretion of cortex in form of "bandages" or patches speaks against a picture of the rhabdosome as a precisely controlled counting device.

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DISCUSSION

N. H. Kirk:

Since I am probably that less patient colleague referred to by Professor Urbanek, I would like to say something in my own defence. In Urbanek and Towe's (1974) publication on dendroid ultrastructure there was no reference to a model for rhabdosomal construction proposed by me in 1972, though this would have provided an instant explanation for many of the tissue relationships described and discussed by them on pp. 11—16.

I therefore felt justified in drawing attention to this in my 1974 publication, and also in correcting those of my 1972 suggestions which were incorrect, having been based on the supposition that cortical and fusellar tissues were separately secreted.

In Urbanek and Towe's (1975) publication on graptoloid ultrastructure there was again no mention of my 1972 model, and although all reference to *Rhabdopleura* had been omitted, there still seemed to be no clear picture of the simple extrathecal evagination which was all that was required to explain the apparent complexities in the ultrastructure.

I therefore produced my 1975 publication, because it seemed sensible to try to clear up the confusion, and because Urbanek and Towe's new ultrastructural data (fully acknowledged in my publication) allowed me to modify and expand many of the ideas formulated in 1972.

In pages 17—20 of this publication (Kirk 1975) the criticism of Urbanek's (1973) hypothesis of organization of graptoloid colonies was directed, not against his gradients of morphogenetic substances as he now seems to imply, but against

his emphasis on the stolon as the conduit along which they spread from the siculozoid. I preferred to regard the mantle of extrathecal tissue as itself providing the changing environment in which the genetic instruction was interpreted, and suggested that "it seemed possible that the incremental secretion (not the graptolite colony as Urbanek puts it) might have constituted some kind of counting device giving precision to biochemical changes occurring with time", what these biochemical changes were, is of course indeterminable. That they occurred with time is not my idea but Thorsteinsson's and Urbanek himself refers to it as "Thorsteinsson's rule" (Urbanek 1973). Urbanek mistakenly applies my description many-mouthed superindividuals to graptolite colonies. Reference to page 19 (Kirk 1975) will show that I applied it specifically to those biserial graptoloids which, in contrast to the continuous variation of a graded thecal series, had complex proximal budding patterns and discontinuously developed colonial organs such as spines, vanes etc. This, to me, suggested the same kind of problem as the differentiation of the tissues and organs in a metazoan individual. While Urbanek finds this simplistic, I find it one of the most difficult problems of zoology.

I do not quite understand Urbanek's meaning when he refers to thecae as showing "frequent isolation (instead of their embedding in common colonial tissue)", and astogeny as "due to budding of zooids with considerable autonomy". Has not Professor Urbanek once again lost sight of the significance of that extrathecal tissue in which the whole colony in all graptoloids and all dendroids was completely embedded and which was responsible for the coordinated secretion of cortex as sheets or bandages irrespective of thecal boundaries, and for such colonial structures as nema, holdfast, vanes etc? Neither do I understand Urbanek's purpose in attributing to me, quite incorrectly, the point of view that "a graptoloid colony is nothing but individual". Maybe it was in order to confront me with his curious corollary that "her gradual biochemical changes occurring with time within internal environment of colony are reduced to trivial processes of aging". Is then the coordinated development of the thecae and various colonial structures, like the differentiation of tissues and organs in a developing metazoan individual, also to be reduced to trivial processes of aging?

I am obliged to Professor Urbanek for having referred to my Publications. I will be pleased to send copies to anyone who would care to read them.