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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Introduction

Recent interest in the study of coloniality owes much to the work of Beklemishev (English translation 1969, and earlier Russian editions). Two important symposia edited by Boardman et al. (1973) and Larwood and Rosen (1979) followed many themes suggested by Beklemishev's work and initiated some new lines of discussion. Beklemishev (1951, 1969) supplied also the modern foundation for studies on the comparative anatomy and the development of bilaterian colonies.

The aim of the present paper is the integration of data and views developed independently in the particular fields of zoological research, concerning the origin and development of colonies in selected groups of bilaterian animals. The study is focused on two groups: on one hand it is based on pterobranchs and closely related graptolites and on the other hand on bryozoans. Pterobranchs indisputably belong to Deuterostomia (Nielsen 2001; Halanych 1995) and usually are placed in the phylum Hemichordata, while graptolites are very closely related to Pterobranchia (Kozłowski 1949, 1966; Urbanek and Dilly 2000). Recent authors believe that both groups should constitute a common class—the Graptolithoidea (Beklemishev 1951, 1969; Urbanek 1986; Mierzejewski and Kulicki 2002). The systematic position of Bryozoa has been more controversial. They have either been grouped with the members of Lophophorata at the base of deuterostomes (Zimmer 1973), or treated as a group of protostomes, displaying transient features to pterobranchs. They share some anatomical similarities with this group of hemichordates (see also Stebbing 1970). Molecular data (18S rDNA) indicate, however, that lophophorates are protostomes and are related to mollusks and annelids to form a provisional group of Lophotrochozoa (Halanych et. al 1995). Similarities with pterobranch hemichordates should be regarded as convergence (Halanych 1996) or a result of parallel evolution from the common ancestors of all Bilateria. Recently, Nielsen (2002: 687) defined bryozoans as "the most puzzling phylum in phylogenetic studies of the Bilateria" but after evaluation of the entirety of morphological data placed Bryozoa with protostomes.

Therefore, it seems safe to conclude that colonialism developed independently in the Graptolithoidea and Bryozoa, each group being related to a different superphylum of Bila-

teria. In this paper the Graptolithoidea (Pterobranchia + Graptolithina) are selected as a key model for comparative studies because they provide the most graphic examples of morphogenesis in colonies and an unsurpassed record of their evolutionary changes. Some of my ideas on the early astogeny of graptolites and bryozoans were presented in November, 2000 on a seminar at the Palaeontological Institute, Russian Academy of Sciences in Moscow and later published (Urbanek 2003).

Graptolites as a model group for studies on bilaterian colonies

Graptolites are a fossil group of hemichordates that lived in the early Palaeozoic, appearing 500 million years ago, and were closely related to still living pterobranchs. Primitive Cambrian representatives of the group were sessile, but their descendants, the true graptolites, known as graptoloids, were planktic, forming the predominant group of macrozooplankton (Figs. 1–3). In the Ordovician and Silurian–Early Devonian seas they were ubiquitous, being represented by rapidly evolving and extremely widely distributed species, a priceless tool for stratigraphic subdivision and intercontinental correlation. Each individual (zooid) in the colony produced its own tube (theca) made of some secreted scleroproteic material (collagen, Towe and Urbanek 1972) displaying a characteristic microstructure due to the presence of minute growth bands called fuselli. This material is capable of preservation in the fossil state. Such fossil skeletal remains, preserved in the form of carbonized stipes or branches, are the primary source of our information concerning the structure and morphogenesis of graptolite colonies.

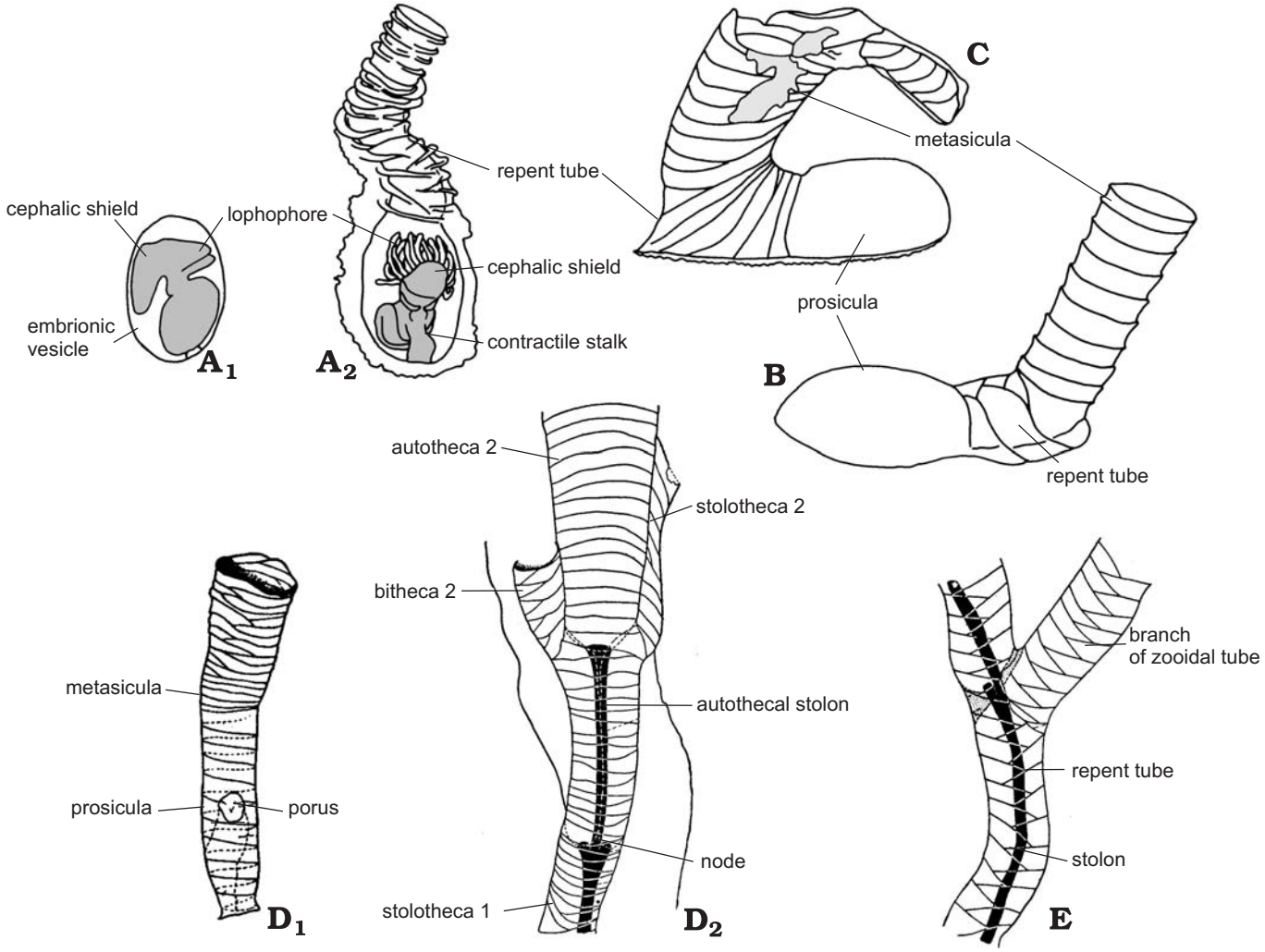


Fig. 1. Astogeny in Graptolithoidea. **A**–**C**. Early development of a rhabdopleurid pterobranch and a tuboid graptolite colony. **A**. Encapsulated larva after metamorphosis (A_1) and primary zooid in *Rhabdopleura compacta* Hincks (A_2). **B**, **C**. Comparison of sicular portions in Recent *Rhabdopleura compacta* (**B**) and in Ordovician tuboid graptolite *Epigraptus* Eisenack (**C**). **D**. Sicula (D_1) and thecae with underlying stolon system (D_2) of an Ordovician dendroid graptolite *Dendrograptus* sp. **E**. Zooidal tubes and internal stolon system in Recent *Rhabdopleura normani* Allman. Not to scale. A, B, from Stebbing (1970), C–E, from Kozłowski (1949, 1970).

Colonies in the majority of sessile groups of graptolites are marked with a distinct polymorphism, while the colonies of planktic graptolites, the Graptoloidea, are monomorphic and have colonies composed of a single type of zooids and thecae. The basic pattern, which is almost universal in sessile orders of Graptolithina, involves differentiation into thecae of three categories: autothecae, bithecae, and stolothecae. Autothecae are the largest and frequently have an apertural apparatus. The bithecae and stolothecae are much narrower, tubular, and devoid of any apertural elaborations. The stolothecae carry inside a section of the stolon that divides at certain points within the parental stolotheca (Fig. $1D_2$). In this way, the stolon produces short branches leading to a bitheca, an autotheca as well as to a daughter stolotheca that contains further extension of the stolon. The bithecae do not contain a stolon and usually are adnate to the adjacent autothecae. Kozłowski (1949) suggested probably the most suitable biological interpretation of thecal differentiation, assuming a distinct sexual dimorphism among zooids: autothecae correspond to fully developed female zooids, and bithecae housing partly reduced male zooids. In addition to this classical view of Kozłowski one could assume that the male zooid in each triad had its sex phenotypically determined, in response for the presence of juvenile female zooids in the stolotheca.

The reduction of male zooids observed in some sessile groups of Graptolithina leads consequently to their elimination in planktic graptoloids. Their thecae are composed solely of autothecae, fused with their proximal portion corresponding to the former stolotheca. Transient forms with colonies still preserving a few bithecae in their distal part are known (so-called anisograptids). Elimination of bithecae was preceded (according to Kozłowski 1949) by transformation of female zooids into hermaphroditic individuals. Therefore, colonies of Graptoloidea were composed of hermaphroditic zooids, essentially monomorphic, but displaying to a various degree the morphological gradient operating along the colony axis.

Early development of sessile graptolites (Dendroidea, Tuboidea) was best recognized and interpreted by Kozłowski (1949, 1963). The development of the colony starts with the sicula, the zooidal tube of the founder zooid, which developed from zygote (Fig. 1C, D_1). It is composed of two clearly distinct parts, which differ sharply in their microstructure: a bottle-shaped or cylindrical prosicula, and a tubular metasicula. These differences were ascribed by Kozłowski, who based his conclusions on bryozoan analogy, to metamorphosis of a free living larva, which produced first the prosicula, and later the metasicula. Thus, the sicula housed a siculozooid, the only sexually produced zooid in the colony (= an oozooid). All remaining zooids originated by budding from the siculozooid. In sessile graptolites it proceeded from the stolon, which initially originated within the prosicula, and emerged from its cavity through an opening called the porus. After this, it penetrated into the initial or sicular stolotheca, inside which occured the first division of the stolon. In the best studied dendroid and crustoid graptolites thecae were produced in triads, each being composed of an autotheca, a stolotheca, and a bitheca.

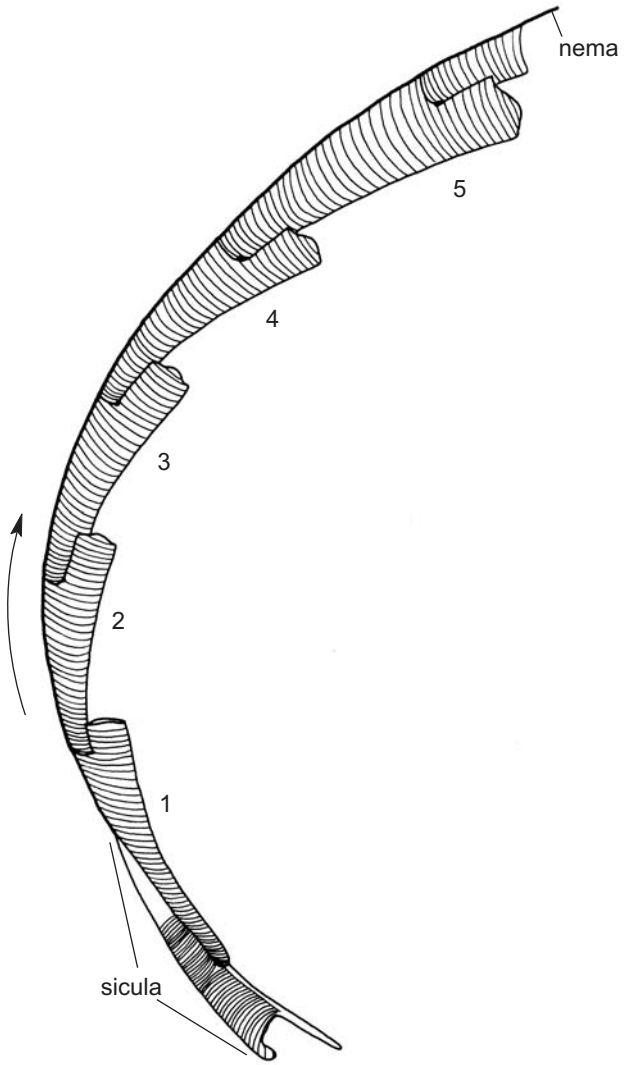


Fig. 2. Diagram illustrating the structure and terminology of a proximal part in a monograptid colony composed of a series of zooids arranged along a single axis. Arrow indicates the direction of colony growth. Note the presence of sicula, the zooidal tube of the oozooid, and a number of zooidal tubes (called thecae, *1–5*), and occupied by asexually produced zooids (blastozooids); the nema is a thread-like prolongation of the apex of sicula, serving as a skeletal axis for the growing colony. Modified from Urbanek (1973).

The early development of graptolites was compared by Kozłowski (1949) with that in rhabdopleurid pterobranchs, which was at that time inadequately known. The presence of two portions, homologous to prosicula ("embryonic vesicle") and metasicula respectively was demonstrated, the latter showing a characteristic "fusellar" structure due to composition of peculiar growth bands. Later studies by Stebbing (1970) and Dilly (1973) provided more details (Fig. 1A). The larva encapsulates itself in a completely sealed vesicle made of skeletal substance. After metamorphosis the juvenile oozooid breaks the wall of the vesicle (so-called perforatory

budding) and starts to secrete the first growth bands of the zooidal tube. This tube is comparable to the metasicula, while the embryonal vesicle resembles the prosicula of sessile graptolites (Fig. 1B, C). In turn the first blastozooid also breaks the wall of the vesicle and starts to secrete its own zooidal tube. The stolon system inside the zooidal tubes of *Rhabdopleura* is strikingly similar to the stolon system recognizad in crustoid, dendroid, and tuboid graptolites (Fig. $1D_2$, E). A more detailed comparison of early developmental stages in extant *Rhabdopleura* and tuboid and dendroid graptolites was given by Urbanek (1986).

Astogeny in most groups of sessile graptolites involves a monotonous iteration of triads (or diads as in Tuboidea), all thecae showing the same size and shape. No polarity or morphological gradient has been observed except in *Mastigograptus*, a primitive sessile graptolite, occupying a transitory systematic position between rhabdopleurid pterobranchs and dendroid graptolites. As revealed by Bates and Urbanek (2003), the stolothecae of *Mastigograptus* display a morphological gradient in size and shape. However, the only large group, which exhibits, as a characteristic feature of its organization, the polar organization of colonies is the planktic Graptoloidea. Thecae (corresponding to the autothecae fused with their stolothecal segments, see above) regularly increase in size distalwards, until they reach the distal type characteristic of zone of astogenetic repetition.

The gradient theory of graptoloid colonies

The most simple (although secondarily simplified, which is irrelevant to us) model of graptoloid colonies can be found in Silurian monograptids (Fig. 2). Their colonies consisted of a single series of individuals interconnected by a string of tissue, homologous to the stolon of sessile graptolites but deprived of a peridermal sheath. They developed by budding from the founder-zooid—the sicula—resembling in essential features the sicula of sessile forms and composed of pro- and metasicula. However, the graptoloid prosicula has many derived features: instead of producing a basal disc it ends with the so-called nema, a thread made of skeletal substance and frequently serving as the axis for the growing stipe. This reflects a morpho-ecological revolution which occurred after transformation of sessile colonies into planktic ones.

There is a striking difference between the theca of this sexually-produced founder-zooid (the oozooid, Fig. 2, sicula) and the thecae of all the remaining zooids, which are its progeny produced by budding, that is asexually (Fig. 2, *1–5*). A graptolite colony is therefore a clone. Consequently, all its members, varying in number from a few to several hundred, share the same genotype. Though this is a fairly obvious conclusion, it had never been formulated before Urbanek's paper published in 1960. And what is more important, the consequences of the clonal nature of graptolite colonies had been overlooked. An

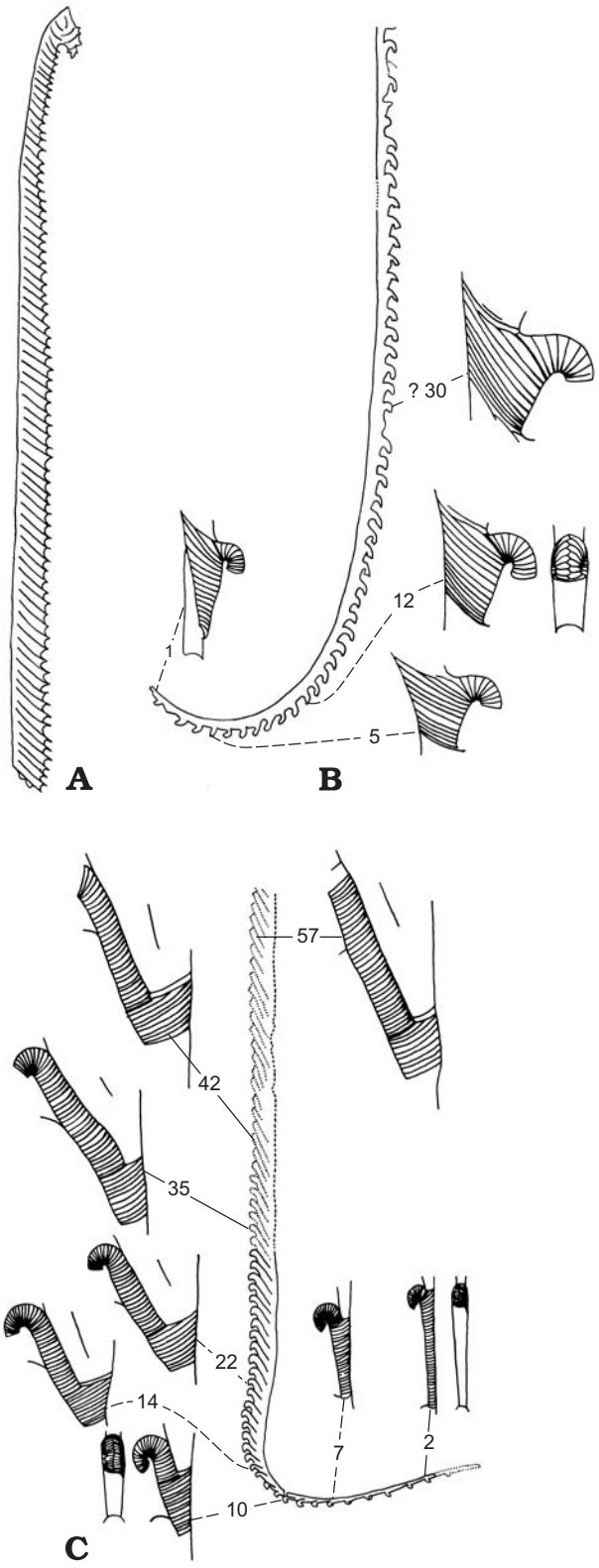


Fig. 3. Variation of morphological characters of zooidal tubes (thecae) along the colony axis. **A**. *Didymograptus pakrianus* Jaanusson, only one branch of the biramous colony presented. **B**. *Monograptus clingani* (Carruthers). **C**. "*Monograptus*" (= *Pernerograptus*) *argenteus* (Nicholson). A, B belong to uniform type and exhibit mainly size gradient, while C represents a biform type, with distinct differences in morphology of proximal and distal thecae. Not to scale. From Urbanek (1973).

important conclusion following from their clonality is understanding the remarkable morphological differences within a single colony merely as variation of the expression of the same genotype. The same conclusion is tenable for bryozoan colonies, which likewise are clonal systems: all zooids represent the progeny of ancestrula produced by budding.

When tracing the degree of expression of a given character (e.g., the degree of curvature) in the successive thecae of a single graptoloid colony we observe a regular, graded change—the expression is at its highest near the proximal (most frequently, Fig. 3C) or the distal (less frequently, Fig. 4A) end of the colony, decreasing gradually towards the opposite pole (Figs. 3C, 4A). This pattern of change is suggestive of a gradient in the distribution of the morphogen, which controls the expression of a given gene or set of genes (Fig. 5C, F). Such was the working hypothesis which I advanced for the first time in my paper published in 1960, and elaborated subsequently in later years (Urbanek 1963, 1973; Urbanek and Uchmański 1990).

All my considerations are based on the remarkable feature of the graptoloid colonies, namely their polar organization: zooids in every graptoloid colony gradually increase in size distalwards (Figs. 3A and 4B). The proximal portion of the colony is composed of the smallest zooids, but their size gradually increases distalwards, until they reach a maximum attainable size in the distal portion of the colony. Further growth consists of the iteration of the thecae of a uniform size and shape (Urbanek and Uchmański 1990). An immediate comparison with simply organized bryozoan colonies comes to mind: in both cases astogeny reveals a proximal zone of astogenetic change and a distal zone of astogenetic repetition as defined by Boardman and Cheetham (1969). Likewise bryozoan colonies, every stipe of graptoloid colony ends with a growth zone displaying an ontogenetic gradient—growing thecae decrease in size distalwards. It seems that the majority of monograptid colonies are open ended, i.e., they are capable of an endless addition of new zooids at the growing tip. However, some graptoloids are definitely finite, and composed of a determined, usually small number of zooids. Finite colonies have their growth zones arrested at a certain stage, their thecae never attain size corresponding to the thecae of the repetition zone. A combination of zone of astogenetic change, with a relatively short zone of repetition followed by arrested growth zone, would result in a "foliate" shape of stipe, so characteristic of phyllograptid rhabdosomes (Urbanek 1973). In extreme cases of colony reduction, exhibited by some retiolitids (e.g., *Holoretiolites*), entire colony may be considered as an arrested growth zone. Therefore, the size of the thecae decreases distalwards exhibiting a fixed ontogenetic gradient. Paper by Kozłowska-Dawidziuk (2004) provides more data on the case in question.

The above mentioned size gradient is usually accompanied by a gradual change in the morphology of some thecal structures, such as different apertural lobes or spines, or variation in the curvature of the apertural part. In some graptoloids, called technically "biform", the thecae in the proximal part of the colony manifest a sharp contrast with those in the distal portion, but these differences are attained gradually by minute modifications in the structure of the successive thecae (Figs. 3C, 4A). This pattern of thecal variation within a single

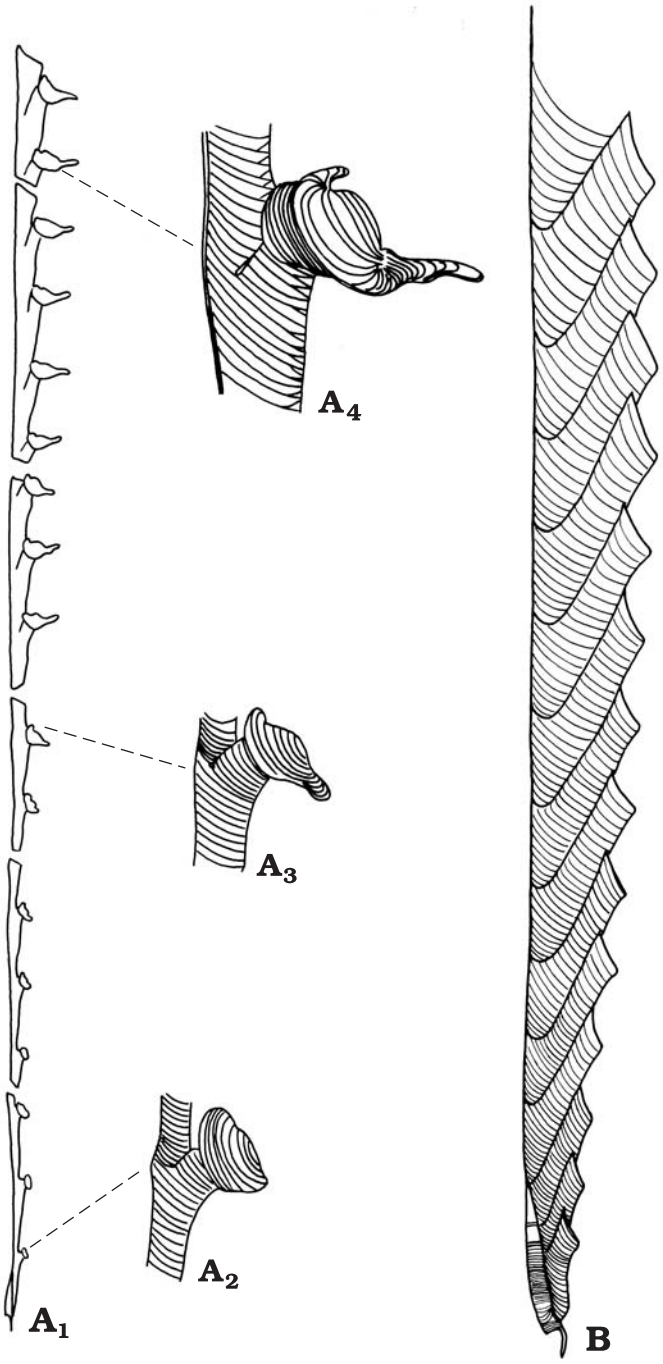


Fig. 4. **A**. Variation of morphological characters of zooidal tubes (thecae) along the colony axis in *Cucullograptus aversus* Urbanek (A_1), details of structure of apertural apparatus within the proximal, medial and distal thecae (A_2–A_4). **B**. *Pristiograptus dubius* (Suess), thecae with growth bands shown diagrammatically. A is a biform type with the strongest expression of characters in the distal part of the colony, while B is a uniform type exhibiting mainly the size gradient. Not to scale. From Urbanek (1973).

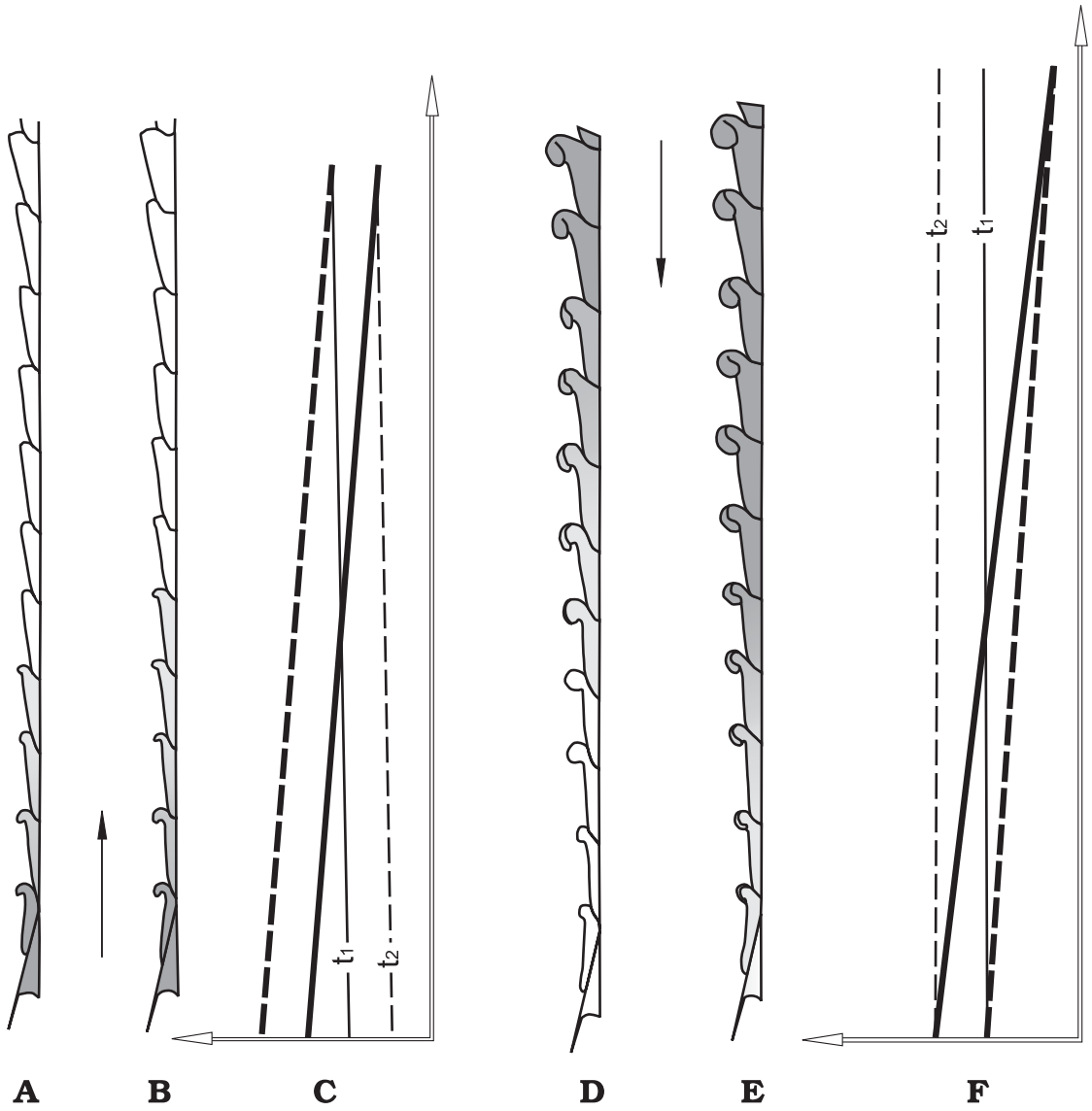


Fig. 5. Diagram illustrating the introduction and spread of new thecal characters in monograptid colonies (**A**, **B**, **D**, **E**) with attempted biological interpretation of evolutionary changes involved (**C**, **F**). **A**, **B**. Proximal introduction and distalward spreading (as indicated by an arrow) of a phylogenetic novelty, interpreted (in **C**) as a result of increasing activity of a morphogen produced by the oozooid (siculozoooid) and acting as a stimulator of a given character, either due to increase of its amount (change from continuous oblique into broken oblique line) at the stable threshold level of the reactivity of the tissue, or due to increase of reactivity of tissues (lowering of the threshold level from t_1 to t_2) at the stable amount of morphogen produced. **D**, **E**. Distal introduction and spreading toward the proximal end (as indicated by an arrow) of a phylogenetic novelty, explained in F as a result of decreasing activity of a morphogen acting in this case as an inhibitor of a given character, either in result of its decreasing amount (change from continuous to broken oblique line) at the stable level of the reactivity of tissues (t_1) or by the rise of the threshold level (t_2) and decrease of their reactivity at the stable of morphogen produced by the oozooid. Note that the expressivity is indicated by the intensity of shading, while penetrance by numbers of zooids affected to any degree. From Urbanek (1960, 1973).

graptoloid colony is strongly suggestive of their gradient nature. What is valid in this respect for monograptids is largely tenable for all graptoloids. My way of thinking was here influenced by the classical ideas of physiological gradients formulated by Child (1915, 1941) and by some later works on the morphogenesis and regeneration in hydroid colonies (corresponding sources were given in Urbanek 1973, and Urbanek and Uchmański 1990). Gradient interpretation introduced a new logic to the understanding of thecal variation in graptoloids, which was otherwise compared with metamerism (see Bulman 1958). The present status of morphogen gradient theory, examples of best known morphogens and patterns of their action are discussed in Gordon and Bourillot (2003).

Following the concept of "morphogen and gradient", I assumed that the morphological gradient so distinctly visible in graptoloid colonies was related to the underlying gradient in the distribution of the morphogenetically active substance (Urbanek 1960, Fig. 5 herein). Other models are also possible: the gradient may be expressed not by the morphogen alone but

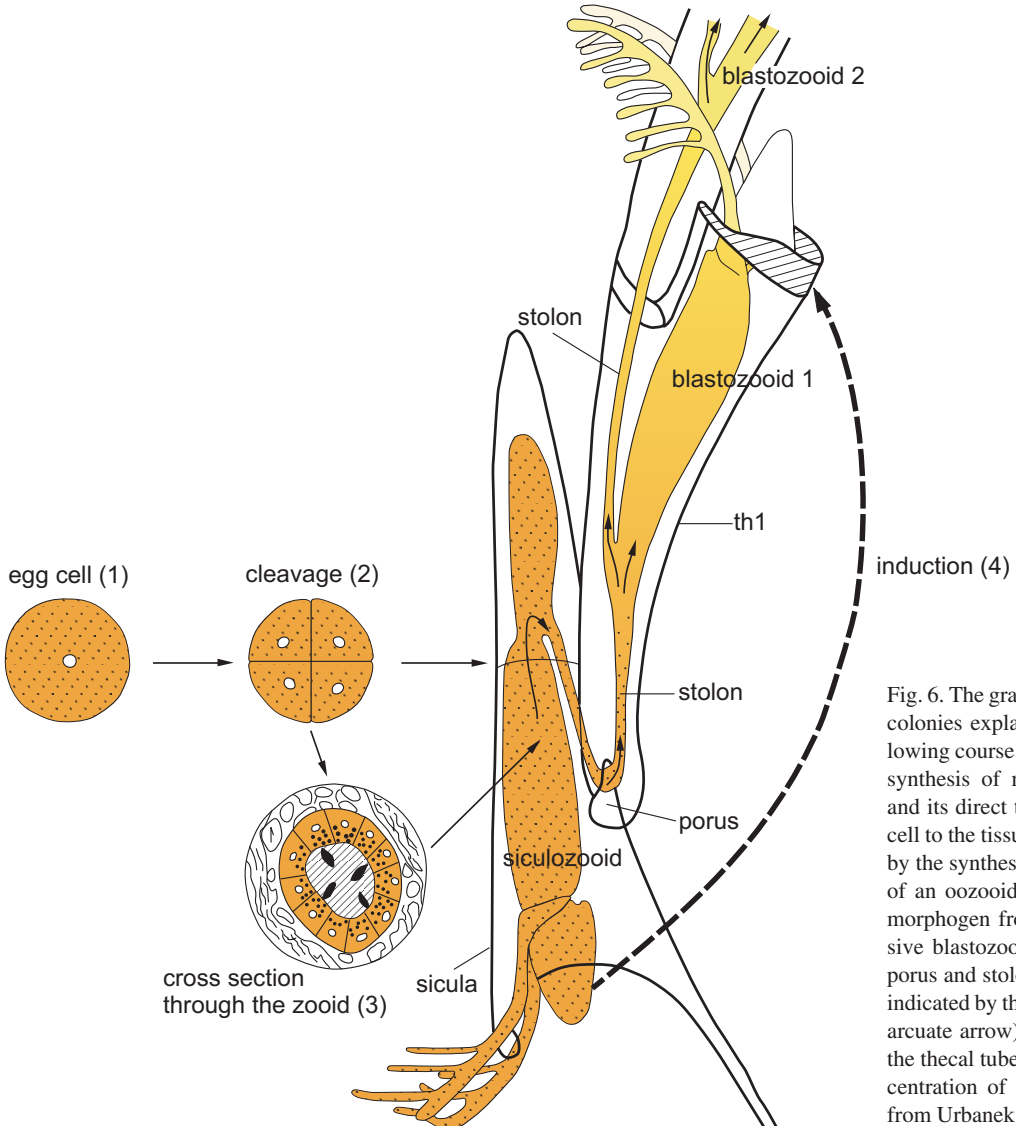


Fig. 6. The gradient theory of organization of graptoloid colonies explains the origin of morphogen by the following course of events: 1–2, prezygotic or postzygotic synthesis of morphogen precursors (probably RNA) and its direct transmission through cleavage of an egg cell to the tissues of an oozooid (siculozooid), followed by the synthesis of the morphogen proper in the tissues of an oozooid (3); diffusion (indicated by arrows) of morphogen from siculozooid to the tissues of successive blastozooids (B_1, B_2,...) by interconnections like porus and stolon and gradual dilution of morphogen as indicated by the intensity of shading; induction (4, thick arcuate arrow) of specific morphological characters in the thecal tube (stippled area on th1) related to the concentration of morphogen at a given zooid. Modified from Urbanek (1960, 1973).

also by the graded change in the position value (competence) of the tissues, there may be two or more morphogens, or even as recently suggested the gradient might be based on decay of mRNA in the produced tissues, causing only secondarily a graded drop in the synthetised morphogen (Dubrulle and Pourquié 2004; Schier 2004). However, the model suggested herein seems most parsimonious, offers minimum of assumptions and may serve as a first approximation.

I also argued that the morphogen was probably produced in the egg-cell or tissues of the founder zooid of the colony, the siculozooid (being at the same time the only oozooid in the colony), and later spread by diffusion producing a gradient effect (see Urbanek 1973, Fig. 6 herein). One of the arguments for this assumption has been the almost certain origin of the siculozooid from a fertilized egg. As long as 40 years ago, I suggested that the morphogen or rather its precursor must have been transmitted from the egg cell. One can hypothetize that the morphogenetic agent, which supposedly defined the spatial organization of graptoloid colonies was either a regular morphogen of zygotic origin or one of the factors synthetized in the prezygotic egg cell, similar to the *bicoid* or *caudal* gene products in *Drosophila* and its homologues in all Bilateria. The crucial role of these genes and their products is widely recognized by contemporary evolutionary developmental biology (Wolpert et al. 1998; Carroll et al. 2001; Davidson 2001). Some of them are anteroposterior (A-P) axis organizers and control the expression of genes along the A-P axis in embryos of solitary organisms. One can expect that similar genes may control also the phenotypic expression in the series of successive zooids which develop by budding from a single parental oozooid in such clonal systems as graptoloid colonies. However, while it seems safe to conclude that siculozooid was the source of morphogen in graptoloid colonies, considerations concerning the intrinsic mechanisms of morphogen nature and action are beyond the scope of the present paper.

As suggested earlier (Urbanek 1960, 1963, 1973; Urbanek and Uchmański 1990), such morphogen produced by the

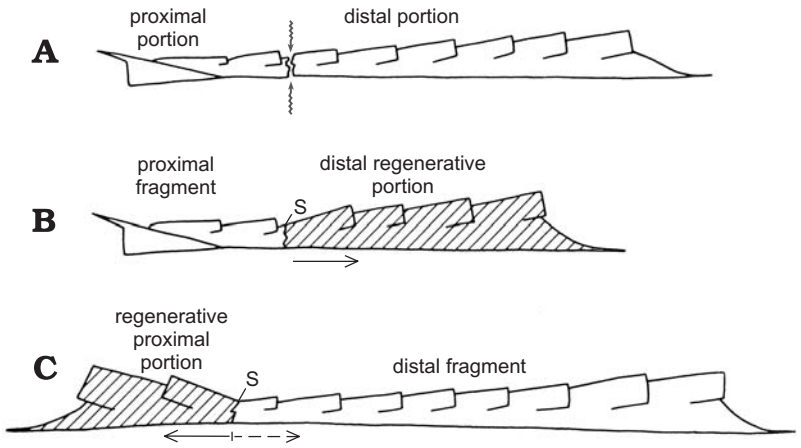


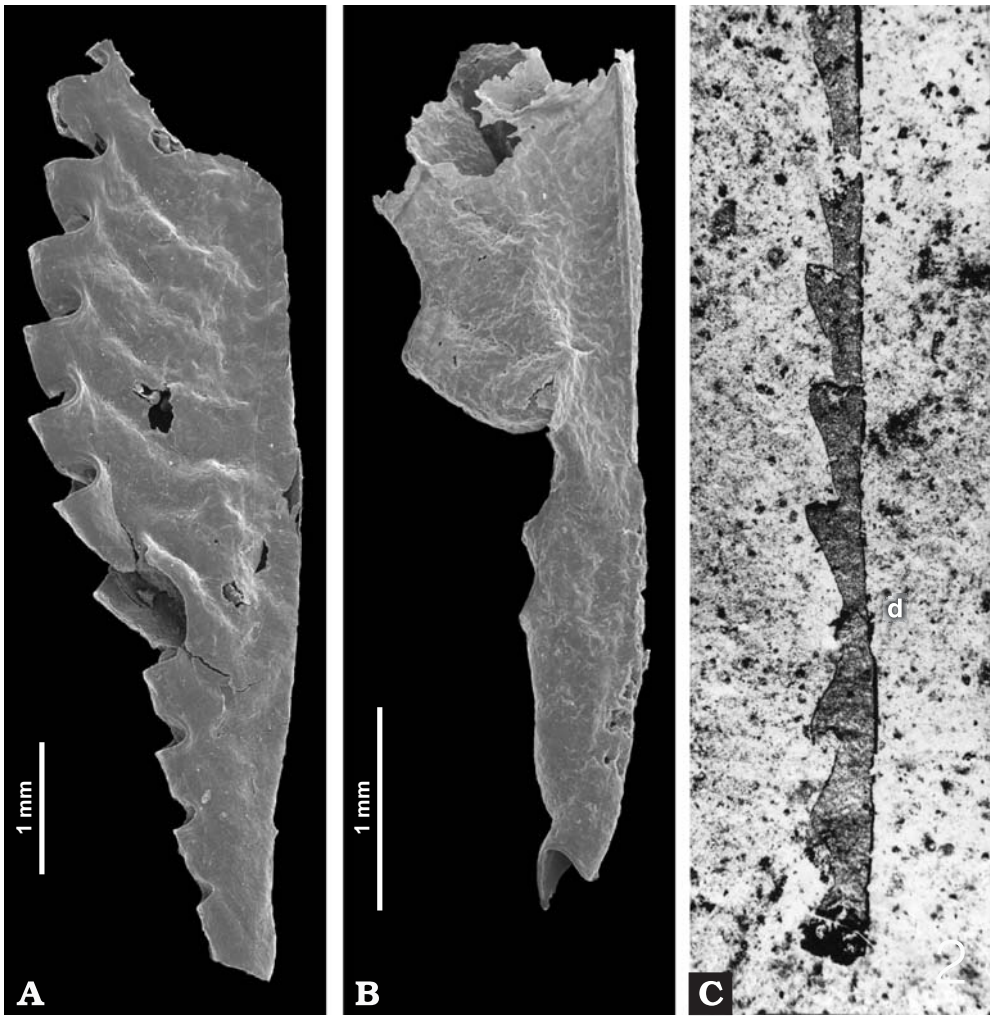
Fig. 7. Diagram showing two patterns of regeneration in fragmented graptoloid colonies. **A**. Primary rhabdosome subject to fragmentation (as indicated by wavy line) into the proximal and distal portions. **B**. Regeneration from the proximal fragment of the primary rhabdosome resulting in a unipolar regenerative morphosis (single arrow), with a distal regenerative portion showing an abrupt increase in the size of zooidal tubes (thecae). **C**. Regeneration from the distal fragment of the primary rhabdosome resulting in a bipolarly growing morphosis (two arrows) due to formation of the regenerative proximal portion growing (solid arrow) simultaneously with the preserved distal tip of the primary rhabdosome (broken arrow); S, scar or traces of fracture, regenerated portions obliquely hatched.

egg cell and/or in the tissues of the siculozooid (oozooid) controls the morphogenesis of the graptoloid colonies. Therefore, a diffusion and gradual decrease in the amount and concentration of the morphogen during the development of the colony has an effect of a morphological gradient along the stipe. We should assume the long ranged and rather long lasting effects of a morphogen in graptoloid colonies, surpassing the scale of action recognized in solitary organisms (Gordon and Bourillot 2003).

When a phylogenetic novelty is introduced from the proximal end of the colony, the morphogen stimulates its expression, while in the case of distally introduced new characters the morphogen behaves as an inhibitor of its expression (Fig. 5). In both cases one could expect a direct relationship between the amount of the morphogen available and the degree of expressivity of a given trait. Urbanek and Uchmański (1990) presented a mathematical model simulating these relations in a growing monograptid colony (see also an attempt at quantification of data by Fortey 1983).

Moreover, the concept of the localization of the morphogen source in the siculozooid has found independent and convincing evidence in the studies on regenerative morphoses observed in the fossil record (Figs. 7, 8). Graptoloid colonies were relatively long tapes suspended in the water column subject to breaking and fragmentation. Some colonies which survived such catastrophic events, were capable of regeneration and were preserved in the fossil record. Thanks to "a little bit of luck", a necessary companion of every palaeontologist, I collected some instructive instances of regenerative colonies. They comprise cases of regeneration from both the preserved proximal part (a genet) as well as the preserved distal fragment (a ramet) of the primary colony (Fig. 7A). In the first case, a regenerative colony consists of the preserved proximal portion of the primary colony displaying a morphological gradient and a regenerative portion made of uniform robust thecae of the distal type (Figs. 7B, 8A, B). Therefore, such colonies display a sharp contrast between the primary part, which developed in the presence of abundant morphogen, and the regenerative one, which developed after the morphogen content dropped down below the threshold level. In the second case, the colonies attained a characteristic bipolar shape, with both the primary and the regenerative part being composed of uniform robust thecae (Figs. 7C, 8C). Such thecae develop under normal conditions in the distal part of the colonies. Nature itself has provided experiments comparable with the cutting of the graptoloid colonies, a method frequently used in laboratory experiments designed to study the morphogenetic potential of a given tissue or organism. Hence, we can say that one can apply experimental methods in palaeontological studies (Fig. 8 herein, for more data on regeneration of graptoloid colonies see Urbanek and Uchmański 1990). Moreover, results of these natural experiments contradict Dzik's (1975, 1981) concept of morphological gradient due to gradual accumulation of nutrients in the tissues of growing colony, which is expressed in progressively larger size of zooids. Regeneration from short proximal fragments that had only a few small zooids and a very low feeding potential produce large regenerative zooids (Fig. 8A, B, D, E). In our case the results of the experiments clearly indicate that the siculozooid was the source of some morphogenetic agent, whose activity gradually decreased to drop eventually below the threshold level of the competence (or the position value) of the tissues. In the light of the entirety of the facts, the gradient theory seems well supported by empirical evidence and is in good accord with the recent theories of morphogenesis.

Further natural experiments are provided by multiramous colonies, displaying a number of simultaneously growing tips. In the case of *Cyrtograptus* Carruthers, the colony is composed of a main branch, corresponding to the regular monograptid stipe, and a number of side branches which develop from the apertures of its certain thecae (Fig. 9A), while in *Neodiversograptus* Urbanek additional branches radiate from the aperture of the sicula (Fig. 9B). Detailed studies on these graptolites (Thorsteinsson 1955; Bulman 1958; Urbanek 1963, 1997) show that such compound colonies display a concomitant growth and thecae near growing tips had the same morphogenetic potential in spite of the fact that they were situated at different distances from the sicula. Urbanek (1960, 1963) interpreted this in the light of the classical studies on plant morphogenesis (Thimann 1932), showing that simultaneously growing tips must have the same amount of growth



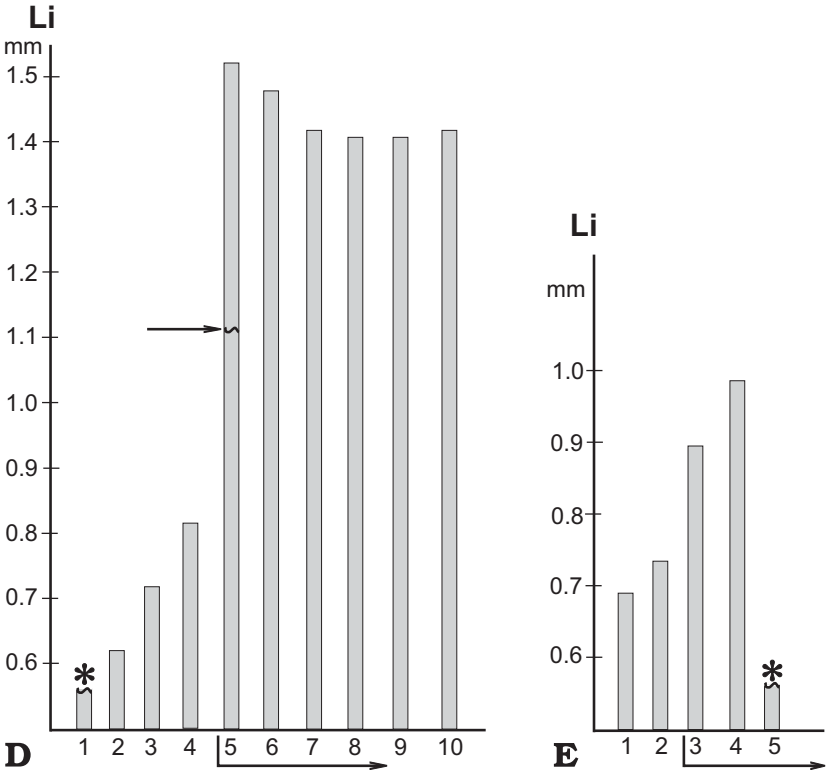


Fig. 8. Regeneration from preserved proximal (sicular) portion of the primary rhabdosome as seen with SEM in Late Silurian monograptids. **A**. "*Monoclimacis*" *haupti* (Kühne). **B**. *Pristiograptus dubius* (Suess), with characteristic sudden increase in width immediately behind a distinct scar. **C**. Instance of regeneration of fractured colony from preserved distal portion of the primary rhabdosome as seen in Late Silurian *Linograptus posthumus* (Reih. Richter) preserved on the rock surface: a bipolar regenerative colony showing contrast in size of thecae on primary and regenerative branch; d point of divergence of two series of zooids. **D**, **E**. Graphs showing length of thecae in regenerated rhabdosomes as illustrated in A and B. The breaking point and direction of regeneration are marked by a broken arrow, asterisks denote strongly damaged thecae, an arrow in D indicates that theca 5 is composed if two portions primary and regenerative one. Specimens A and B reproduced after Urbanek and Uchmański (1991) were etched from the Mielnik I.G. 1 bore-core: *"M." haupti* depth 912.10 m, top of *C. aversus* zone; *P. dubius* depth 922.10 m, *S. leintwardinensis* zone; C from Urbanek (1973), Chełm borehole, depth 1554.50 m, *Neocolonograptus lochkovensis* Zone, approx. × 15.

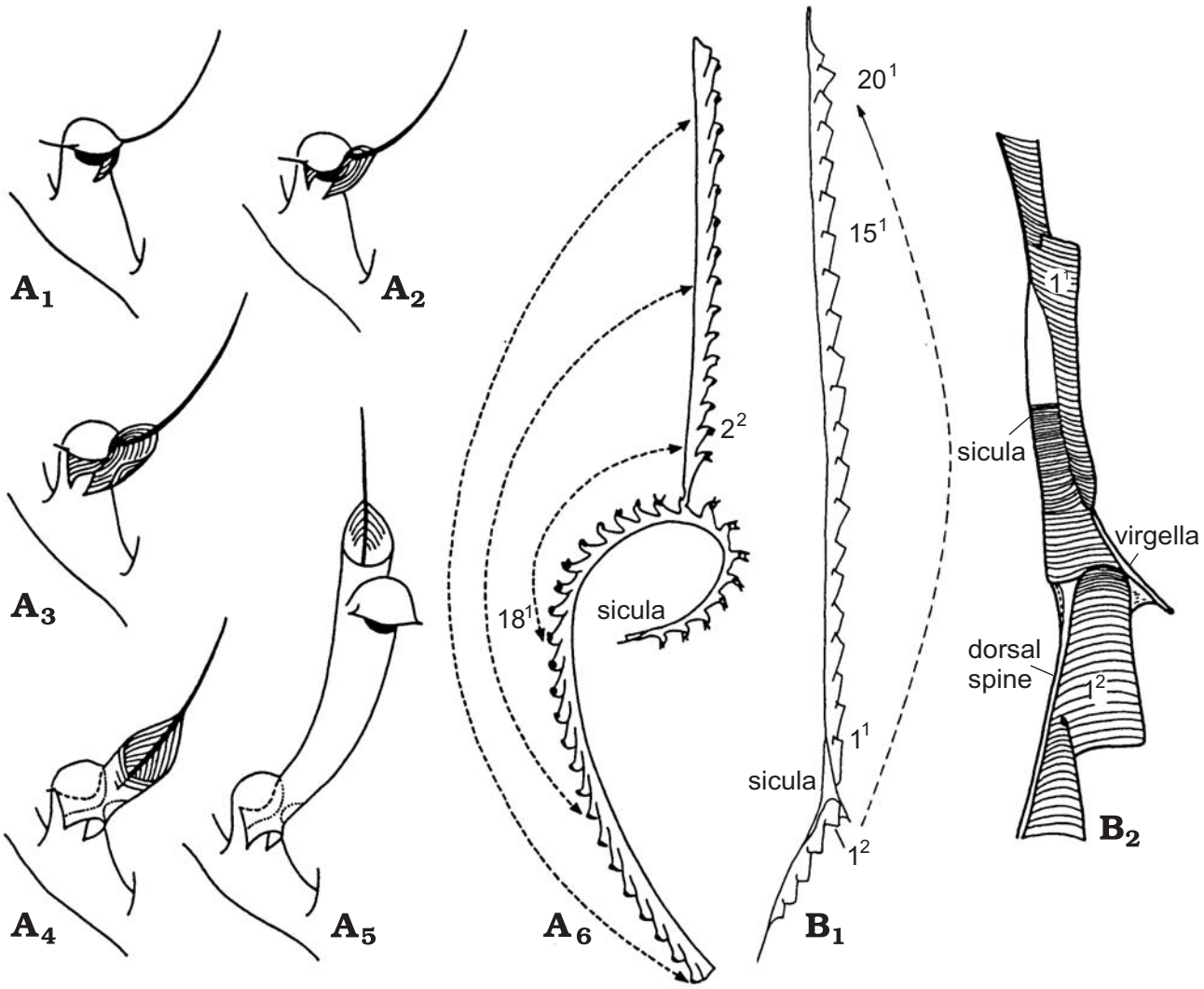


Fig. 9. Growth relations in compound monograptid colonies. **A**. Cladial generation in *Cyrtograptus rigidus* Tullberg, showing successive stages of budding of lateral cladium from aperture of a mother theca on the main stipe (A_1–A_5) and a mature rhabdosome with isochronous thecae showing the same size and shape interconneccted by broken lines (A_6). **B**. Delayed formation of a sicular cladium in *Neodiversograptus nilssoni* (Lapworth), where its first theca (1^2) is isochronic with thecae 15^1–20^1 of the primary stipe (B_1) and therefore first theca of the sicular cladium (1^2) much more robust than the first theca of the primary cladium (1^1) (B_2). Not to scale. A, after Thorsteinsson (1955); B, from Palmer (1971) and Urbanek (1963).

hormone (auxin), otherwise growth in one of the tips will be inhibited. *Mutatis mutandis*, such regularity is tenable for graptolite colonies (and was named the "Thorsteinsson rule" by Urbanek 1960)—thecae formed at the same time (isochronous) have the same size and shape (are isomorphous), because as we can infer, the amount of morphogen available during their budding was the same. Hence, the first theca of the primary stipe (1^1) and the first theca of the sicular cladium (1^2) in *Neodiversograptus* display a sharp contrast because they are formed at a different time (Fig. 9B), while in the phylogenetically more advanced *Linograptus* Frech both resemble each other, because both are growing simultaneously (Urbanek 1963, 1996). One can conclude that multiramous graptoloid colonies were balanced morphogenetic systems regulated by distribution of some morphogene, which attained an equal level on concurrently growing tips.

When tracing the phylogeny of gradient organization in Graptolithoidea we see the disparity of this feature of astogeny. There are no traces of morphological gradients in Rhabdopleuroidea, but distinct traces of them were detected in Mastigograptina. This latter group has transient features between rhabdopleurids and dendroid graptolites. This may indicate for a latent polarity of the colonies in all Graptolithoidea. This latent polarity was probably created by production and distribution of some morphogen in the prezygotic or zygotic egg-cell. Only in some cases has this underlying polarity been expressed phenotypically. This is the case in the Graptoloidea, where morphological gradients are a characteristic feature of astogeny in the entire group. The reasons for this are not obvious—some authors (e.g., Finney 1986) suggested that morphological gradients create distinct differences between the proximal (juvenile) and the distal

(mature) portion of the rhabdosome. Due to different hydrodynamic properties this may be an agent enabling the segregation of juvenile and mature colonies in the water column. This, however, most probably, was not the only function of morphological gradient.

Phenogenetics of astogeny

As already mentioned, an important conclusion following from the clonal nature of graptolite colonies is understanding the remarkable morphological differences within a single colony merely as variation of the expression of the same genes. This observation was the starting point of my considerations (Urbanek 1960, 2001) when I realized that the concepts of expressivity and penetrance introduced by Timofeef-Ressovsky (1931, 1934) may be applied to the evolutionary changes observed in graptoloid colonies. Expressivity is the measure of the severity of the phenotypic effect, while penetrance is a number of individuals having a gene and expressing it to any measure. One of the elementary changes in these colonies is the appearance and spreading throughout the colony of a new morphological trait in the structure of the zooidal tubes (thecae). A frequently observed novelty in the thecal characters is curvature displayed as a gradual change from a straight tube to a curved (hooked) one. A considerable variation in the degree of expression of this and many other characters may be seen in successive thecae along the axis of the colony (Figs. 3, 4). Such changes indicate changes in expressivity of certain genes in the development of a single colony. Moreover, when tracing changes of a given theca (say, No. 1 or 3) in sequential species (chronospecies) of a lineage, we frequently observe an increase in the degree of curvature, from almost straight to strongly hooked, or even coiled. Such changes are suggestive of changes in expressivity, as defined by Timofeef-Ressovsky, of a given character (phene) in the course of phylogeny. High specificity of many traits (such as position of rostral processes, left—or right asymmetry of apertural lobes) seems to indicate that the morphological differences in thecal characters within a single colony are merely variation in the expression of the same genes. Thus, the proximal to distal variation in the degree of hypertrophy of the left apertural lobe as observed in the astogeny of *Cucullograptus hemiaversus* (Urbanek 1960) can be best explained as a different expression of the same gene or gene set. Argument that the proximal and the distal thecae may express different genes seems very unlikely.

As one can expect, such phylogenetic novelties make their first appearance either from the proximal or from the distal end of the colony (Fig. 5A, D). As has been traced in numerous lineages by a great number of students, the newly-appeared characters are primarily expressed only in a few zooids, situated at one end or the other of the ends of the colony. Further evolutionary changes involve gradual spreading of the novel character (frequently an apomorhic feature) distal- or proximalwards, respectively. Therefore it becomes expressed in a greater number of zooids (Fig. 5B, E). Moreover, the highest observed degree of expression of a given morphological character also increases (Fig. 5A, B, D, E)). These phenomena, recorded by generations of palaeontologists engaged in the study of graptolites, provide, in my opinion, a strong analogy to penetrance, another notion defined by Timofeef-Ressovsky (1931, 1934). There is a remarkable similarity between graptolite problem and the problem Timofeef-Ressovsky was facing when studying the expression of the *vti* gene affecting the veins on wings in the *Drosophila funebris.* There was a difference, however. In order to ensure that the given recessive gene is really present in all individuals of the studied experimental population Timofeef-Ressovsky was obliged to use strict inbreeding of F2 homozygotes. In graptoloid colonies this condition is given *a priori* due to the asexual reproduction from a single zooid, playing the role of the founder of the colony.

Another element of the model suggests the presence of the threshold effect (Urbanek 1960, 1963, 1973; Urbanek and Uchmański 1990). A drop in the amount of the morphogen below a certain level results in the absence of the phenotypic effect. It is obvious that the position of the threshold defines the number of zooids displaying phenotypically a given trait, and in this way it also determines the penetrance of a given gene in the graptoloid colony. A direct comparison with primary zones of astogenetic change and primary zones of astogenetic repetition as recognized in bryozoan colonies (see below) is possible—and there is little doubt that they also represent a threshold effect.

An analysis of the evolution in numerous graptoloid lineages indicates that changes in both expressivity and penetrance are involved. Moreover, in graptoloid colonies high expressivity is corelated with high penetrance and *vice versa.* In other words, expressivity and penetrance display a special spatial pattern being subordinated to the gradient organization of the colony. Speaking in terms of modern developmental biology, the distribution of the morphogen supplies positional information to particular zooids defining their way of expressing their genes.

Moreover, in the light of the recent views on the morphogenesis of the graptolite skeleton, it should be considered an external structure, roughly comparable to honey combs, spider webs etc. In other words, like the skeletons in extant pterobranchs, they were secreted by the zooid's glandular organ, the so-called cephalic disc (Crowther 1980). Therefore, we must assume that the morphogen provided merely a signal controlling the secretionary behaviour of the zooids and resulting in a specific and position-depending structure of the zooidal tube.

The morphological gradient hypothesis met with different opinions from graptolite specialists. Some considered the idea as sufficiently stimulating (Bulman 1970; Berry 1987; Fortey and Bell 1987). Some were criticizing this theory as inadequate (Rickards 1978), probably because the mere concept of morphogen was misunderstood by them (see Urbanek

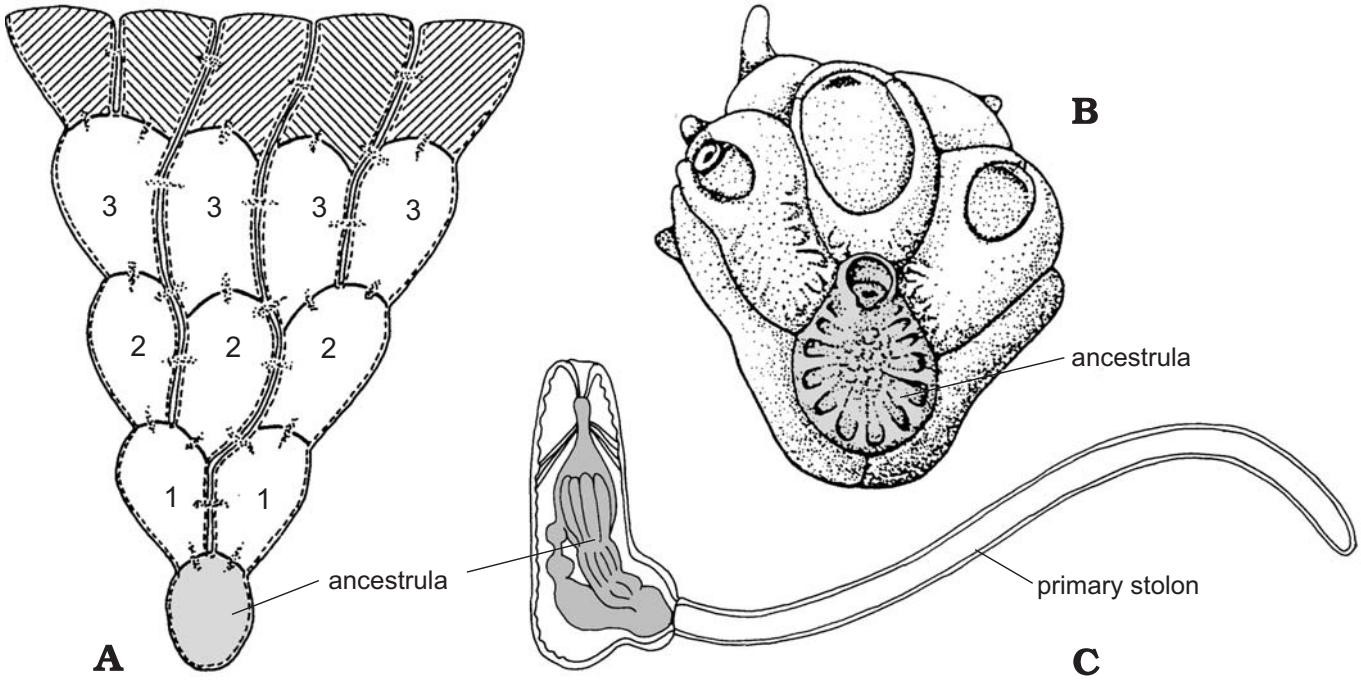


Fig. 10. Ancestrulae and early astogeny in bryozoan colonies. **A**. Idealized diagram showing organization of a gymnolaemate bryozoan colony, 1–3 successive generations of blastozooids. **B**. Early stage of astogeny in a colony of a Recent ascophoran cheilostomate *Metrarabdotos*, showing ancestrula and three autozooecia placed immediately distally to it. **C**. Ancestrula of a Recent ctenostome *Amathia lendigera* with a stolon on which all new buds will generate. Not to scale. A, from Cheetham (1986); B, from Cook (1973); C, from Zimmer and Woollacott (1977).

and Uchmański 1990: 57). Gould (1977) reviewed Urbanek's papers (1960, 1966, 1970) and accepted his view that thecal evolution results from changes in a morphogenetic substance produced by the sicula. However, his attempt to reduce evolution of graptoloid colonies to heterochrony as a "primary determinant" seems misleading—it neglects the clonal nature of graptolite genets. Dzik (1975, 1981) commented on the morphogen hypothesis and has suggested an entirely different approach, discussed herein on p. 492 in connection with regeneration of graptolite colonies. Hammer (2000) discussed the inhibitory interaction between adjacent stipes in multiramous colonies (diffusion of nutrients or pheromones) as a possible mean of morphogenetic control on colony development—a point raised earlier by Fortey and Bell (1987).

Towards a new interpretation of astogeny in bryozoan colonies

Bryozoan colonies differ from the previously discussed colonies of Graptolithina in a number of ways. Some of these differences are an obvious consequence of the systematic position of both groups (see above), while others are more specific. The latter include an epithelial secretion of the skeleton (instead secretion by the glands of the cephalic disc in pterobranchs and presumably in graptolites) and its strong mineralization (as compared with purely organic skeleton in all hemichordates), the substantial role of chitin as fabric of the cuticle and matrix of the mineral skeleton (as compared with proteinaceous, mostly collageneous, nature of the skeleton in hemichordates, Towe and Urbanek 1972; Armstrong et al. 1984). Because of the epithelial mode of skeletal secretion the morphogenetic signal in bryozoans is directly transmitted to the growing tissues, while in pterobranchs and graptolites it is transmitted as a positional information *via* secretionary behaviour of the zooids.

Polymorphism of zooids in bryozoan colonies is much more elaborated as compared with an incipient polymorphism observed within autothecae in some groups of sessile graptolites (see for a detailed comparison Urbanek 1986). Because of the polymorphism of most bryozoan colonies, their astogeny is a much more complicated process and is reflected in a parallel way in particular morphs. In the present paper considerations are based on the astogenetic changes in the autozooecia, where these changes are most distinct and best known. Also the pattern of budding of succeeding astogenetic generations is in bryozoan colonies more differentiated as compared with colonies of Graptolithoidea. Stolons are present in some bryozoan groups but it seems that their morphological nature differs from that in Graptolithoidea.

Yet in spite of these distinct differences there are also remarkable similarities in the general organization of colonies in graptolites and bryozoans. They are most expressed in the general pattern of astogeny.

In the normal course of astogeny (Fig. 10), bryozoan colonies are commonly founded by a single primary zooid (ance-

strula), fully comparable with the sicula of Graptolithina in its origin from the zygotic egg cell through the larval metamorphosis. In the Cyclostomata the attached larva (preancestrula), occupying the bottle-shaped part of the prinary zooecium transforms into the ancestrula proper which produces the tubular portion of it (Zimmer and Woollacott 1977).

Also fully comparable is the astogenetic role of the primary zooid in both groups, exhibited in the asexual production of zooids according to various budding patterns. However, the resemblance between the sicula of Graptolithina and the ancestrula of Bryozoa, although very important for biological interpretation, cannot be evaluated as homology. In both cases these similarities reflect merely the course of metamorphosis of the free living larva, a process which probably developed independently in each group as a result of parallelism or convergence (Kozłowski 1949).

The ancestrula, not unlike the sicula in graptolites, morphologically differs more or less markedly from the asexually produced zooid, which in turn are, *mutatis mutandis*, fully comparable with blastozooids in graptolite colonies. In some bryozoans metamorphosis of the oozooid is followed by simultaneous formation of a pair of primary zooids (double or twin ancestrula) or even a greater number of first generation zooids morphologically so similar, that none of them could be regarded as ancestrula proper. However, such primary zooids, as it follows from the course of astogeny, play the role of a composite ancestrula. Generally speaking, bryozoan colonies correspond to the genets (as defined by Harper 1981) and display for this reason many features in common with graptolite colonies which are of the same nature, although their modules are in each case quite differently organized.

The asexually produced zooids of bryozoan colonies, which develop from ancestrula, usually display more or less conspicuous generational differences in morphology. Commonly these astogenetic differences are restricted to the proximal parts of the colony, while its distal parts are characterized by several generations of zooids of repeated morphology. This simple pattern of colony organization, common in cheilostome colonies, resembles essentially the pattern observed in graptoloid colonies. Moreover, the astogenetic changes seen within the proximal part of bryozoan colonies display a distinct gradient, expressed in uniform progression distalwards in general size and in a number of structural details of zooecia. In cheilostome colonies best studied in this respect, these changes include besides the increase in size also the gradient of complexity in number of spines or costae, and in the complexity of oral and other skeletal structures. This part of the colony was termed by Boardman and Cheetham (1969) the primary zone (or stage) of astogenetic change. It includes the primary zooid (or zooids) and the group of immediately budded zooids, and therefore comprises relatively few generations and a small total number of zooids. The primary zone of astogenetic change is followed by the primary zone of astogenetic repetition (Boardman and Cheetham 1969), which consists of zooids with uniform size, morphological characters and pattern of budding. This zone

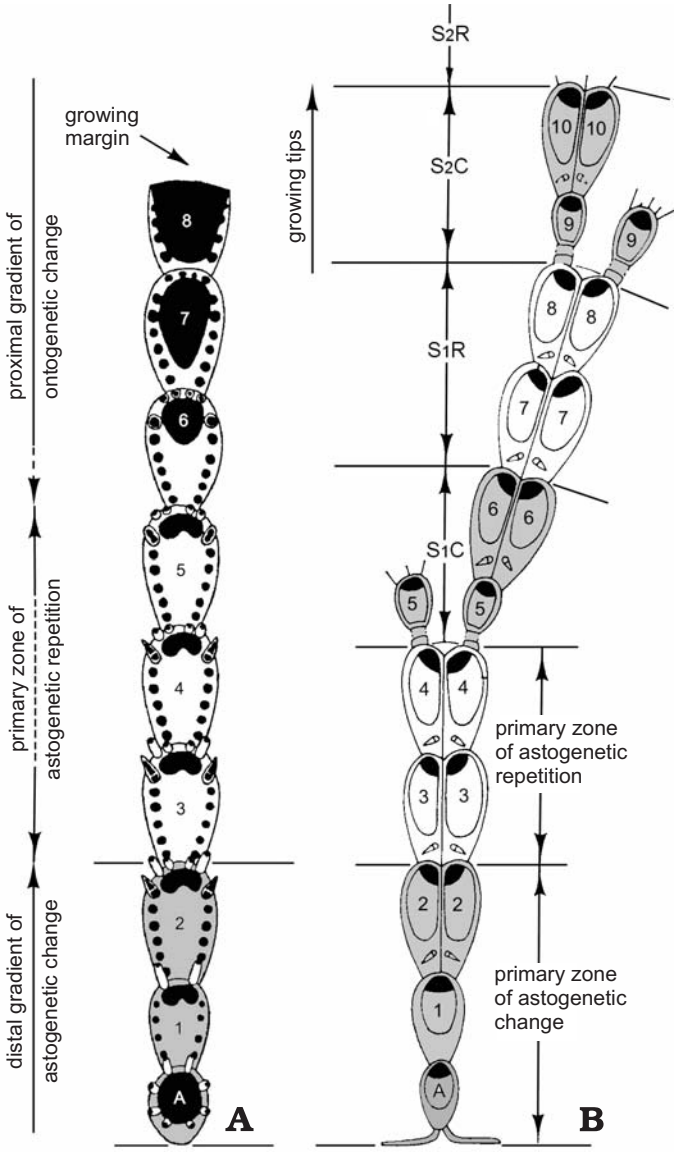


Fig. 11. Astogeny of bryozoan colonies. **A**. Diagram based on *Escharoides* Milne Edwards and showing morphological variation in relatively simple bryozoan colony. All zooids have originated from the primary oozooid (A, ancestrula) and display a gradient in size and shape of zooecia until first repetitive zooids appear (3). This proximal series of zooids compose together the primary zone of astogenetic change. Further development leads to a series of zooids showing the same size and shape and making the primary zone of astogenetic repetition. A series of zooids near the growing edge (5–8) display a growth gradient, all of them will reach eventually morphology displayed by 4. **B**. Astogeny in a cheilostomate bryozoan *Poricellaria* d'Orbigny showing besides primary zone of astogenetic change and repetition, also cyclically repeating subsequent zones of change (S1C, S2C) as well as of repetition (S1R, S2R). While primary zone of astogenetic change begins with the ancestrula (A) subsequent zones of astogenetic change start with diminutive zooids which are not wholly comparable with ancestrula. In the given zone of astogenetic repetition zooids are alike and their morphology repeats this of the last generation of the preceding zone of astogenetic change. Successive zones of change occur over fewer generations, their zooecia become longer, more asymmetrical, may also change the budding pattern. Modified from Boardman et al. (1969).

comprises many generations and therefore also the vast majority of zooids in the colony. Distally, bryozoan colonies end with a growth zone composed of zooecia showing an ontogenetic gradient (Fig. 11A).

Bryozoan colonies which display this pattern of zonation may be easily compared with previously described monograptid colonies (Fig. 12). Thus, the primary zone of astogenetic change corresponds to the proximal portion of graptoloid colonies showing a distinct morphological gradient in the size and shape of thecae. Both in graptoloids as well as in bryozoans this gradient may be explained as a correlate of the underlying gradient in the distribution of morphogen, produced by the oozooid (sicula and ancestrula, respectively). The primary zone of astogenetic change represents this band of bryozoan colonies where the amount (or concentration) of the presumed morphogen introduced from the egg cell *via* ancestrula is above the threshold level of the reactivity of zooidal tissues. It follows from my reasoning that the primary zone of astogenetic repetition would represent this band of the bryozoan colony where budding and growth of zooids proceeded below the threshold level of the morphogen concentration. This band fully corresponds to the most distal part of graptoloid colonies, produced by iteration of thecae with the same size and shape. As already stated, the zone of astogenetic change in bryozoan colonies is a rather short interval of colony, comprising only a few generations of zooids. Bryozoans as compared with graptoloids made in the evolution of their colonies a rather limited use of the opportunities opened by the morphogenetic gradient.

At the present state of knowledge the presence of morphogen produced by an oozooid is purely hypothetical, but its presence is implied by the comparison of events related to development of colonies from the sexually produced ancestrula and through regeneration from colony fragments (ramets). In each case, morphological gradients in the proximal part of normal colonies appear only in the presence of the ancestrula, which developed from the zygote, while colonies developed from fragmented colonies and therefore lacking an ancestrula, do not display morphological gradients. This reflects a remarkable difference between genets and ramets and in turn is in full accord with the observations on fragmentation and regeneration of graptoloid colonies described above (p. 492). In the course of regeneration from colony fragments (usually fragments from larger zone of astogenetic repetition of such colonies) in free-living cheilostomate *Cupuladria*, most regenerated colonies lack a primary zone of astogenetic change (Boardman and Cheetham 1973). In some cases, however, zooecia of the regenerated part of the colony are initially distinctly smaller attaining only gradually the size typical of the primary colony (Bałuk and Radwański 1977, 1984). Therefore, an abrupt change into large sized zooecia, as one might expect by analogy with monograptid colonies, is not observed.

It seems safe to conclude that in bryozoans the presence of morphological gradients (= primary zone of astogenetic change) seems in most cases directly related to the process of sexual production of the primary zooid of the colony. However, some bryozoan colonies, which develop asexually from encapsulated dormant bodies called statoblasts, begin with a primary zooid that can have some morphological features different from those budded from it. Therefore, such colonies are classified technically by most bryozoologists as having a primary zone of astogenetic change. However, because there is no real gradient of changes except for this single difference, the conclusion that they grow without astogenetic change seems more justified.

Otherwise the variety of astogenetic pattern known in the Bryozoa (Boardman 1983; Cheetham and Cook 1983) includes colonies where generational changes are observed throughout the colony life (as in conescharelliniform bryozoans described by Cook and Lagaij 1976). No graptolite analogy can be immediately mentioned, except perhaps secondarily reduced (dwarfed) colonies of retiolitids. However, most gymnolaemates display colonies composed of a primary zone of astogenetic change and a primary zone of astogenetic repetition. The presence of bryozoan colonies with the above simple pattern of astogeny is especially significant for interpretation of their morphogenesis. Most probably they represent a common pattern of astogeny within the group, and in my opinion, their development may be explained in the same way as we try to explain the astogeny of graptoloid colonies.

As bryozoan colonies are clones, they are genetically uniform and the morphological differences observed in expression of certain characters in the course of astogeny (such as size of autozooecia, number and length of spines) may be hypothetically explained in the same way, as it has been suggested for graptoloids (change in expressivity and penetrance of the genes within the same genotype). Until now, the available evidence for the appearance of new characters and trends in the astogeny of bryozoan colonies is inadequate. Moreover, it must be remembered that the bryozoan primary zone of astogenetic change comprises only a few zooids, and one cannot expect effects comparable with magnificient thecal variation in graptoloids. Because of remarkable polymorphism of zooids observed in some bryozoan groups, one can suppose that generation of different polymorphs involved different sets of genes from the common genotype. Thus an avicularia or a vibraculum may turn on a gene set never turned on in an autozooid. This situation is quite different from the pattern of thecal variation seen in the graptoloid colonies, where the morphological differences may be ascribed to the variation of the expression of the same gene set (p. 495).

It is not surprising then when discussing a possible extrapolation of Urbanek's gradient theory onto bryozoan colonies Boardman and Cheetham (1973) stressed empirical similarity of astogenetic changes observed in graptoloid colonies to that in bryozoans within the primary zone of astogenetic change. However, they have found a number of difficulties in application of theoretical explanation suggested by Urbanek to bryozoan colonies. First of all, while in graptoloids the morphogenetic substance is inferred to diffuse from the oozooid distally, resulting in differentiation of morphology between gen-

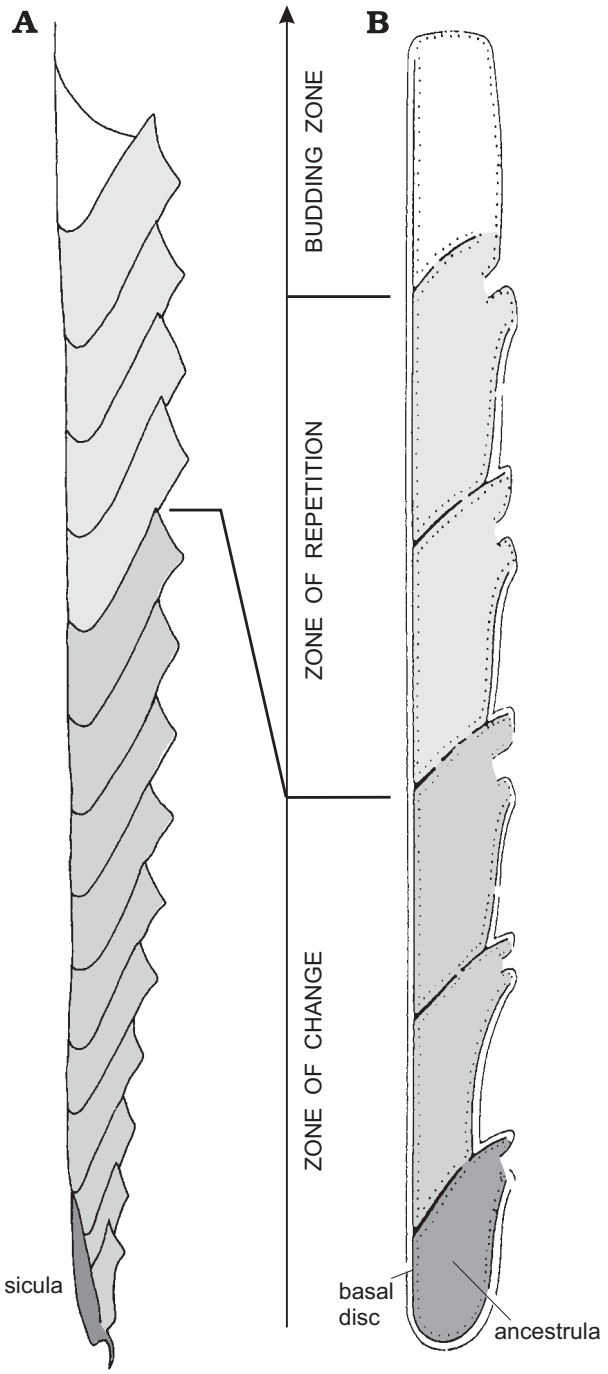


Fig. 12. Comparison of simply organized colonies of a monograptid graptolite (**A**) and a cheilostomate bryozoan (**B**). In both instances colonies originated from an oozooid (sicula or ancestrula) and display a primary zone of astogenetic change (morphological gradient present), followed by a zone of primary astogenetic repetition (no morphological gradient). Colonies end with a terminal growing tip (**A**) or growth zone (**B**). A, original, B, modified from Boardman and Cheetham (1973).

erations throughout the colony, in Bryozoa, the primary zone of astogenetic change comprises only a small number of asexually produced generations "and thus any morphogenetic substance produced by primary zooids appears not to have been continuously diffused throughout colony development" (Boardman and Cheetham 1973: 130). This conclusion of Boardman and Cheetham neglects the postulate suggested by Urbanek, namely a gradual attenuation of morphogen, until it reaches the sub-threshold level. In fact, the distal part of graptoloid colonies is fully comparable with the primary zone of astogenetic repetition in the bryozoan colonies, assuming in both cases a threshold effect in the reactivity of blastozooid tissues. Further, Boardman and Cheetham (1973: 130) argued that "in some stenolaemate Bryozoa soft-tissue connections of the primary zooids to asexually produced zooids are apparently interrupted during calcification", and this again indicates a lack of continuing morphogenetic control by the primary zooids. However, available data indicate that the time required for the action of a morphogen is of short duration (Gordon and Bourillot 2001). Therefore morphological gradients observed in the proximal part of bryozoan colonies in my opinion could be most reasonably explained by the action of some morphogen diffusing from the ancestrula and transmitted during the short period of bud formation (blastogeny). There is no need to assume a continuous diffusion of the morphogen during the entire astogeny. Recent studies (Bates and Urbanek 2003) on the Ordovician sessile graptolite *Mastigograptus* reveal that the sicula in many adult colonies is occluded, yet in spite of this they display a distinct morphological gradient in size and shape of stolothecae (an exceptional case among sessile graptolites). It is obvious that morphogen was released earlier, from still active siculozooid.

Studies by Dzik (1992) on the evolution of Ordovician rhabdomesid bryozoans provided an instance of application of gradient theory assuming an increase of the activity of the morphogen produced by ancestrula. Some authors proposed certain modification of the gradient theory in order to explain the patterns of astogenetic variation observed in bryozoan colonies. Thus origin and growths of monticules, being a sort of subcolonies in trepostome bryozoans, were explained by the presence of the secondary founder zooids. They were assumed to reproduce at certain locations within the colony, being the source of growth substances which controlled the morphogenetic activity around the monticular centers. The astogenetic variation resulting from the activity of ancestrula is considered to be of minor significance (Anstey et al. 1976; Pachut and Anstey 1979).

Cyclicity in late astogeny of bryozoan colonies

However, it seems that some patterns of the late astogeny of bryozoan colonies constitute the main stumbling block on application of the morphogen gradient theory to the colonies of Bryozoa. Thus Boardman and Cheetham (1973) emphasize the common occurrence in Bryozoa of subsequent zones of astogenetic change, which develop distally of the primary zone of astogenetic repetition and can appear many times in sequential order, being each time succeeded by a corre-

sponding subsequent zone of astogenetic repetition (Fig. 11B). Such zones of subsequent astogenetic change and repetition were described in some species of Cheilostomata (Boardman et al. 1970) and in many stenolaemates. This cyclic pattern is doubtlessly an important feature of astogeny in many bryozoan colonies but finds no analogy in the development of colonies in Graptolithoidea.

Moreover, sequential morphological differences between generations in late astogeny, as emphasized by Boardman and Cheetham (1973: 130) can not be controlled by the primary zooids, "which indeed, may no longer have been alive when subsequent zone of change developed". The last conclusion is correct for the late astogeny, but cannot be regarded as adequate for the early astogeny of bryozoan colonies. In my opinion, the primary zonation in bryozoan colonies may be best explained by assuming certain morphogenetic control by primary zooid, while isochronous zonation observed in later astogeny may be best interpreted by taking into account somatic and reproductive cyclicity, so characteristic for the life of Bryozoa in general. There is also a considerable literature dealing with the influence of environmental factors on the growth of bryozoan colonies. Evidence for seasonality of polypide recycling and sexual reproduction in Antarctic cheilostome bryozoans has been provided by Barnes and Clarke (1998), when Pätzold, Ristedt, and Wefer (1987) recognized growth bands made of less calcified zooids and reflecting water temperature changes in an anascan cheilostome from the Irish Sea. Distinct growth check lines were recognized by many authors on bryozoan colonies from different environments and are usually ascribed to seasonal cessation of growth. Although at the present state of knowledge the zonation observed in late astogeny of bryozoan colonies cannot be related with certainty to any known instance of somatic or reproductive cycle (which include i.a. such events as oogenesis, embryogenesis, degeneration and renewal cycles in zooids, Ryland 1979), a correlation of zones of zooids with the same morphological characteristics with succession of certain physiological events in the bryozoan colonies is, in my opinion, highly probable.

The most characteristic of such processes is the degeneration/dormancy—regeneration/renewal cycle. This is clearly indicated by Abbot (1973) in her studies on repetitions in astogeny of the genus *Hippoporina*. She has distinguished two types of growth pattern in bryozoan colonies. In Type A colonies zooids are budded in an uninterrupted, continuous growth sequence from ancestrula to the zone of primary repetition, and further until death or dormancy. In Type R colonies budding proceeds from dormant zooids and is discontinuous, interrupted by one or more cycles of colony dormancy and regeneration. These events are reflected in the morphology of zooids in such a way that provides a basis of differentiating astogenetic growth phases or zones, which are analogous to the sequential zones of change and repetition as defined by Boardman and Cheetham (1969, see also their opinion on Abbot's results in Boardman and Cheetham 1973: 174).

Analysis of factual data provided by Boardman et al. (1970) indicates that category of subsequent zones of astogenetic change and repetition comprises rather different instances of morphogenetic changes which are probably of different nature and might imply different causation. First of all, subsequent zones of change and repetition may be either wholly sequential or in part concurrent. From the instances discussed by Boardman et al. (1970) the example of *Poricellaria* d'Orbigny (Fig. 11B) belongs to the former category, while example of *Bugula* Oken (Fig. 13) illustrates a change from primary repetition into a secondary change only in one branch, while others continue the budding pattern and morphology characteristic of the zone of repetition. The former case is suggestive of a factor widely distributed in the colony or in the environmemt why latter indicates its local, sectorial, nature. It seems clear that only a wholly sequential pattern, which implies the change of the entire growing edge, might be considered as a normal budding pattern and deserve the name of an astogenetic zone (or stage). In my opinion such late astogenetic zones may be ascribed to certain somatic or reproductive cycles in the life of the bryozoan colonies, which affect also the growing edge. Moreover, as recognized by Boardman and Cheetham (1986: 40) "correlated cyclic growth within a group of zooids is not necessarily a result of colony control, but may be simultaneous separate responses to a cyclic environment".

In contrast the concurrent (non-isochronous) changes will result in a sectorial, rather than zonal distribution of morphogenetic changes, and as such do not imply the existence of a distinct astogenetic stage of the colony. They may be stimulated by microenvironmental accidents. The latter may include such factors as crowding, overgrowth, substrate irregularities (Abbot 1973; Boardman and Cheetham 1986). Thus, the local change of growing zooids, from a morphology characteristic of zone of repetition to that of secondary change, may be in some cases microenvironmentally induced (e.g., by obstruction to growth). Although the zooid wholly comparable to ancestrula is lacking in the subsequent zones of change, nevertheless zooecia resemble the earliest generations in the colony, so one can speak on certain reversion in morphology. Moreover, when the essential similarity between ancestrula and particular zooids appearing late in the astogeny and initiating a succeeding zone of astogenetic change is well established (as in the case of anascan cheilostome *Rhabdozoum wilsoni*, described by Cook and Bock (1994) one could perhaps hypothesize on certain effects of rejuvenation, related probably to the reproductive cycle and induced by hormonal agents. To my knowledge such phenomena are unknown in Graptholithoidea and seem to be a unique feature of astogeny in bryozoan colonies.

It seems that the early and late astogeny in bryozoan colonies have different causation: while the former is probably related to the sexual origin of the founder of the colony and as we can suppose to the morphogen produced by it, the latter reflects merely responses to physiological or environmental cyclicity in life of the colony. However, some new aspects of

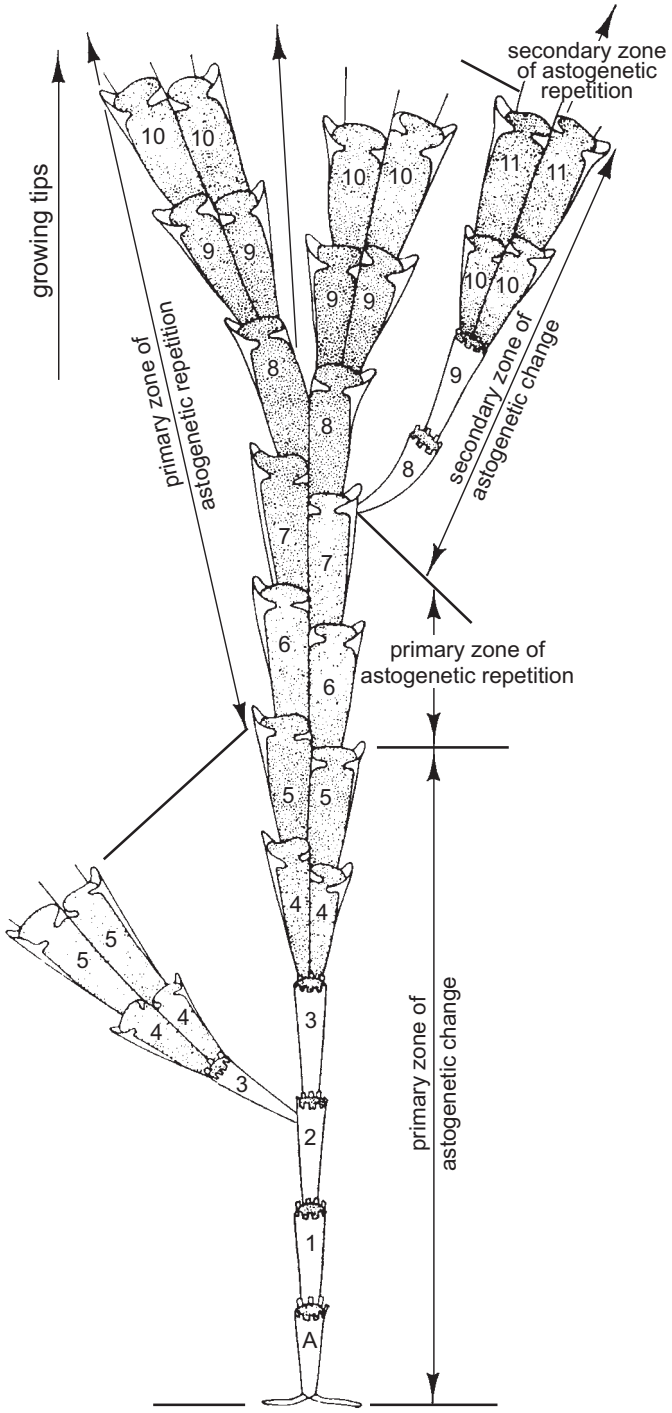


Fig. 13. Diagram of astogeny in the cheilostomate bryozoan *Bugula* Oken showing a regular succession of events, namely a primary zone of astogenetic change and a primary zone of astogenetic repetition as well as the secondary zone of astogenetic change on a separate branch which is concurrent with ongoing primary zone of astogenetic repetition on the main sequence. Astogeny includes here a change from uniserial to biserial budding, while subsequent zone of change is not concomitant but sectorial. Modified from Boardman, Cheetham, and Cook (1970).

astogenetic changes in bryozoan colonies were considered by Taylor (1988) in connection with his detailed studies on anascan cheilostome *Herpetopora*. That study reveals a distinct astogenetic variation, although, the application of the "zone of change + zone of repetition" concept to the case in question seems inadequate. The colony of *Herpetopora* consists of two 1st order branches and a number of higher order branches. Each separate branch in the colony exhibits an astogenetic gradient and the same is true for the whole colony which may perhaps be in perpetual astogenetic change (Taylor 1988: 540). According to Taylor (1988: 546) the astogenetic changes were most likely caused by a morphogen released not from the ancestrula but from the parental zooid of each new branch. This interpretation resembles that by Amstey et. al. (1976) mentioned above. Both suggest an ability of bryozoan colonies to produce secondary founder zooids (a kind of "pseudoancestrulae"), capable of secreting a morphogen. However, at present this idea is no less speculative than the primary concept of morphogenetic activity of ancestrula. Thus at present two main approaches were offered in order to explain secondary astogenetic changes in bryozoan colonies: cyclic factors of life history for isochronous zones and "pseudoancestrulae" for colonies with non-isochronous zones. These differences in approach exist mainly because the physiological basis of astogenetic gradient is completely unknown in living bryozoans (Taylor 1988: 545).

But in general bryozoans as an extant colonial group, are the most suitable model organisms for investigating the causes of astogenetic gradient in Bilateria.

Conclusions

In the light of the recent views on the classification and phylogeny of the animal kingdom, coloniality in hemichordates and bryozoans developed independently. Because of the early schism of the Bilateria into the Protostomia and Deuterostomia, both colonial groups are separated by a distinct morphological cleft. In each case their colonial organization arose on a different structural foundation, from presumably solitary ancestors and by simple means of iterative budding. Nevertheless, colonies of bilaterian animals reveal certain common features of organization. They may be defined as genets, that is clonal systems composed of a sexually produced first zooid (the oozooid as the sicula in the Graptolithoidea and the ancestrula in the Bryozoa). and a series of physically connected blastozooids, which originated by budding, are subject to common morphogenetic control, and share a common genotype. In the light of the theory of modular organization of animal colonies advanced by Harper (1981), blastozooids correspond to modules, repeatable (but not necessarily identical) units, deprived of genetic individuality.

The development of the colony may be reduced to the process of fertilization responsible for the origin of the oozooid, and a long series of mitotic divisions responsible for the rest of the astogeny, especially for the formation of blastozooids (= modules). In this way, we may conclude that there is an essential similarity between the astogeny (devel-

opment of the colony) and the ontogeny (individual development of solitary organisms) in respect of the morphogenetic mechanisms involved. There is little specificity in the organization of the bilaterian genets; in fact, they share a number of common biological properties even with plant genets. The structural characteristics of modules are, however, in each case highly specific and dependent on the phylum from which the colonial forms were derived. This model of colonial organization probably may be extrapolated to colonies of Entoprocta, which are also clonal systems (genets) composed of an oozooid subject to metamorphosis and series of blastozooids, budding from a type of stolons. However, a better knowledge of their astogeny is needed for a safe conclusion.

Bilaterian colonies display a latent polar organization, frequently expressed in a regular morphological gradient. This gradient may be explained by diffusion, over the long axis of the colony, of a morphogen produced by the zygotic founder-zooid of the genet. The hypothesis that the patterns of budding and graded morphological differences among zooids observed in the early astogeny are under control of the morphogen produced by the oozooid seems to be consistent with the entirety of facts available for hemichordate and bryozoan colonies. In my opinion, the gradient of morphogen *per se* has hardly any adaptive significance. The origin of this gradient may be seen as a sort of a side effect of sexual process leading to the formation of the founder zooid. The latter developing as a regular bilaterian animal contaminated the neighboring blastozooids with the products of its own morphogenesis, which certainly included products of genes controlling the body axes. Therefore, we may expect that morphogens responsible for patterning of bilaterian colonies are related to the products of genes responsible for the anteroposterior control of embryos in all solitary Bilateria (Hox, zootype genes). However, once created, the morphogenetic gradient could be used by selective forces to produce various effects, i.a., phenetic differences among zooids of the colony. In a given environmental context such differences might attain certain adaptive significance.

Hemichordate and bryozoan colonies are genetically uniform and all zooids of a single colony share the same genotype. The genetic uniformity may be considered a common feature of colonial organization, with a notable exclusion of tunicate colonies, where zooids with different genotypes might be present within a single cormus (Sabbadin 1979). Hence, in respect of genetic uniformity bilaterian colonies may be divided into genetically uniform (majority of cases) and genetically differentiated (probable exceptional cases). Therefore, astogenetic variation and morphological evolutionary change in the majority of bilaterian colonies may be best described in terms of phenogenetics, that is through the severity or measure of the relative degree of the expression of a given character (expressivity) and the number of zooids affected by it (penetrance, percentage of phenotypic effect). In accordance with the colony's polar organization, phylogenetic novelties are introduced from either its proximal or distant end. Progression of phylogenetic novelties may be interpreted as increasing penetrance of genetic factors. In the evolution of graptoloid colonies changes in penetrance and expressivity are functions of the gradient in the distribution of the morphogen which supplies positional information to the growing zooids. A similar set of notions may probably be applied to the trends observed in bryozoan colonies but the knowledge of relevant details is inadequate.

The hypothesis concerning the source and role of the morphogen was corroborated by observations on regeneration of fragmented graptolite and bryozoan colonies. They revealed that the colonies which developed in the course of a normal astogeny (in the presence of an oozooid) and display an astogenetic change, have their regenerated portions (lacking of an oozooid) always devoid of such change. However, it is clear that the problem in question may be satisfactorily solved only by the use of modern experimental techniques elaborated within the "Evo-Devo" program.

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