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Generation of bilateral symmetry in Anthozoa: A model

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Abstract

Polyps of Anthozoa usually display bilateral symmetry with respect to their mouth opening, to their pharynx, and in particular to the arrangement of their mesenteries. Mesenteries, which are endodermal folds running from the apical to the basal end of the body, subdivide the gastric cavity into pouches. They form in a bilateral symmetric sequence. In this article I propose that early in polyp development the endoderm subdivides successively into three different types of compartments. A mesentery forms at the border between compartments. Two of the compartments are homologous to those of Scyphozoa. They form by mutual activation of cell states that locally exclude each other. The third compartment leads to siphonoglyph formation and is an evolutionary innovation of the Anthozoa. The mechanism that controls the number and spatial arrangement of the third type of compartment changes the radial symmetry into a bilateral one and occasionally into a different one. The dynamics of its formation indicate an activator–inhibitor mechanism. Computer models are provided that reproduce decision steps in the generation of the mesenteries.

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Keywords: Cnidaria; Bilateral symmetry; Evolution; Pattern formation; Mathematical model

1. Introduction

Polyps of Cnidaria share several features: Their body is tube-shaped; at the apical end they have a mouth opening surrounded by tentacles, and at the basal end there is a basal disc or a connection to other polyps if the polyps are members of a colony (Fig. 1). The body wall consists of two epithelial layers, the ectoderm and the endoderm. Interspersed between the epithelial cells are various other types of cells. The two layers are separated by an extracellular matrix, called a mesoglea. Polyps of the various taxonomic groups have various architectures. Polyps of Hydrozoa and Cubozoa have a uniform gastric cavity. In contrast, the gastric cavity of Scyphozoa and Anthozoa is subdivided by folds of the endodermal epithelium. Such a fold is called a septum or mesentery. Mesenteries run from the apical end of the body to the basal end. Scyphozoa usually develop four mesenteries. Anthozoa develop between eight and more than a hundred.

In general, polyps of Anthozoa display a bilateral symmetry. The most dorsal and ventral positions, respectively, are usually occupied by a pair of so-called directive mesenteries. The ectodermal tissue of the pharynx that happens to be opposite to the endoderm between the pair of directive mesenteries produces a band of cilia (called a siphonoglyph), which drives water into the gastric cavity even when the central part of the mouth is closed. A closed mouth forms a line, at both ends of which a hole with a siphonoglyph opens. The line may even be closed permanently (Wilson, 1889, cited in Pax, 1914). Wilson took this observation as support for a theory by Sedgwick (1884) proposing that the mouth and the anus of Bilateria evolved from an elongated blastopore that closes in its middle part.

The bilateral symmetry of Anthozoa is particularly obvious during mesentery formation. Repeatedly, two mesenteries synchronously form to the right and left of an axis that runs from the most dorsal to the most ventral position (sagittal axis). The mesenteries form in couples or pairs, like an image and its mirror image, right and left of this axis.

In Actiniaria initially two mesenteries form synchronously, subdividing the uniform gastric cavity asymmetrically

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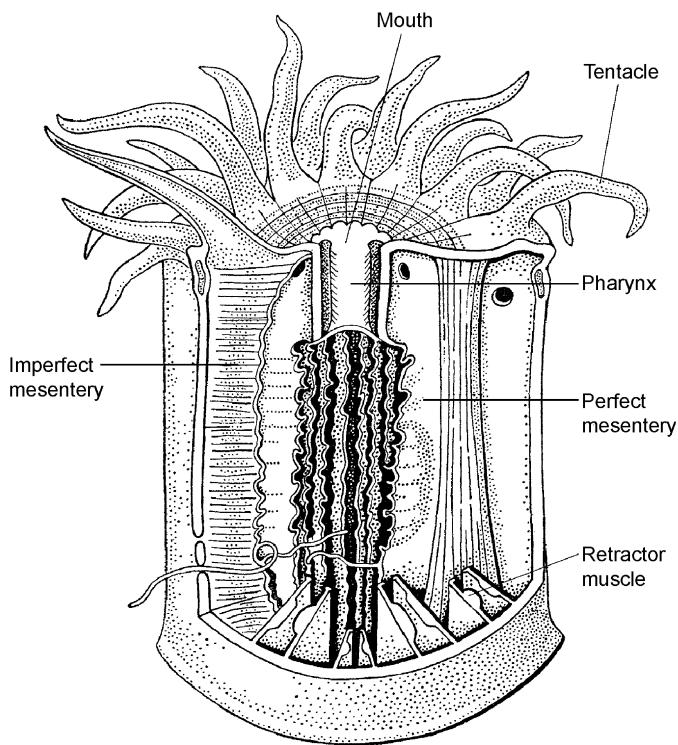


Fig. 1. Solitary Anthozoa polyp (Actiniaria). Section of a polyp displaying mouth, pharynx, and perfect (right) and imperfect (left) mesenteries in the gastric cavity. The swelling at a sectioned mesentery represents the retractor muscle (after Kästner, 1984, p. 227).

(Fig. 2). The smaller part is called the ventral side, the larger is called the dorsal side. Appellöf (1900, cited in Pax, 1914) found that mesenteries do not form by a branching of the mesoglea but rather from the activity of the endodermal epithelia, which grow, form a fold, and then produce mesoglea in between. The next two mesenteries also form synchronously. They are directive mesenteries. These two directive mesenteries form at the most dorsal position. In the next step two directive mesenteries form at the most ventral position. Then, at both sides of the dorsal pair of mesenteries, a further mesentery forms. Thus the temporal sequence of mesentery formation from dorsal to ventral is 2,4,1,3 (Fig. 2). With the formation of these mesenteries, the Edwardsia stage is reached, so-called because of its similarity with the number and arrangement of the mesenteries in the adult *Edwardsia*. All larvae of Actiniaria are said to go through this stage (Doumenc and van Praet, 1987). Mesentery formation up to this stage is rapid. The next four mesenteries usually form after a resting period of a few days to several weeks (Doumenc and van Praet, 1987). They form in variable sequence (2,4,5,1,6,3 or 2,4,6,1,5,3) and often synchronously. At this point the animal has reached the so-called Halcampoides stage.

The 12 gastric pouches can be classified into three types: one exocoel and two different types of endocoels. In 6 pouches additional mesenteries form in the development that follows the Halcampoides stage (Fig. 3). A pouch of this type is called an exocoel. Each of the 6 exocoels is

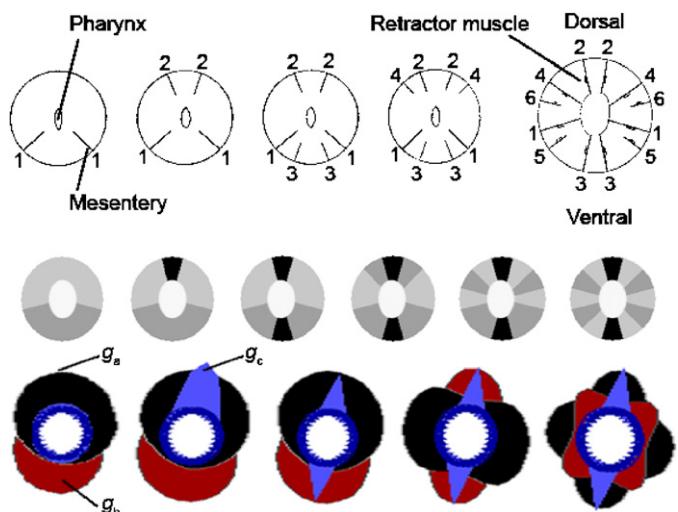


Fig. 2. Mesentery formation in Actiniaria. Upper row: depiction of a cross-section of a developing polyp, displaying the sequence of mesentery formation in Actiniaria (from Pax, 1914, after Lacaze-Dutiers, 1872). Mesenteries at positions 5 and 6 usually form synchronously. The swelling at a mesentery represents the retractor muscle (compare with Fig. 1). Middle row: proposed sequence of compartment formation: Light gray, gastric pouch with endoderm made of Endo A cells (Endo A compartment); deep gray, Endo B compartment; black, Endo C compartment. Initially the uniform endoderm (Endo A) is subdivided into two pouches made of Endo A and Endo B cells, respectively. This results in the formation of a pair of mesenteries. In the depictions of the upper row, these mesenteries are denoted by "1." Then an Endo C compartment forms in the center of the Endo A compartment. In the upper row, the respective mesenteries are denoted by "2," and so on. Lower row: a simulation of the sequence of compartment formation in 30 cells arranged in a cycle. Above the various cells is shown the concentration of the activators g_a (black), g_b (red), and g_c (blue), with g_c in the foreground and g_b in the background. The figures result from a simulation of Eqs. (1), (2), (3a), (4), (5a), (6a), and (7) by a successive reduction of the diffusion constants from $D_{ga} = D_{gb} = D_{gc} = 0.1$, $D_{sa} = D_{sb} = D_{sc} = 0.4$ to, finally, $D_{ga} = D_{gb} = D_{gc} = 0.003$, $D_{sa} = D_{sb} = 0.01$, $D_{sc} = 0.05$. The other parameters are kept constant: Removal rates: $\beta = 0.01$, $\gamma = 0.01$, $\varepsilon = 0.02$, $\phi = 0.011$, $\kappa = 0.01$, $\mu = 0.01$; basic production: $\rho_1 = 0.001$; $\rho_2 = 0.0001$; constants: $\alpha = 0.01$, $\delta = 0.02$, $\zeta = 0.01$, $\lambda = 0.03$, $\eta = 0.04$, $\varphi = 0.1$.

separated from the next one by an endocoel. There are two types of endocoels. One is lined by two directive mesenteries (Fig. 3). Two such pouches exist. The other 4 display no special differentiation. This classification is not arbitrary. In several species, the tentacles display a pouch-specific size and form. Further, their time of appearance and their speed of growth are often pouch-specific (for review, see Pax, 1914, 1925; Doumenc and van Praet, 1987).

Among the various taxonomic groups, the sequence of mesentery formation is different and usually group-specific. Fig. 4 shows an exception: The specimen shown belongs to the Actiniaria but the temporal pattern of mesentery formation is group-specific for Madreporaria (Chevalier, 1987). Figs. 4 and 5 show early mesentery formation in Ceriantharia, Zoantharia, Antipatharia, and Octocorallia.

The challenge is to explain why mesenteries form only in even numbers and why they form in couples and pairs in a

certain sequence right and left of a plane of symmetry (the sagittal axis). The gene activities so far observed do not correspond to the morphological patterns (Matus et al., 2006). For Scyphozoa, Berking and Herrmann (in press) have proposed that the endoderm subdivides into stripes (called compartments) that run from the apical to the basal body end. Where cells of different compartments meet, they form a mesentery. It is obvious that mesenteries can only form in even numbers. The term *compartment* is used because these tissues share properties with the tissues termed compartments in other organisms. Cells of a compartment form a continuous sheet. In general, following cell division in the descendants the state of the

compartment is maintained. However, under certain conditions a group of cells can switch into a different state. Scyphozoa polyps are argued to have two different endodermal compartments, which form by “lateral activation of locally excluding states” (Meinhardt and Gierer, 1980; Meinhardt, 1982). Each of the two cell states is controlled by a specific activator that stabilizes that state. Cells of each state produce a diffusible substance that cells of the other state need to maintain their own state, and a common repressor brings about the local mutual exclusion of the two states. The architecture of the gastric cavity of Anthozoa is much more complex and usually displays a bilateral symmetry. Thus, additional mechanisms can be argued to operate in Anthozoa polyps.

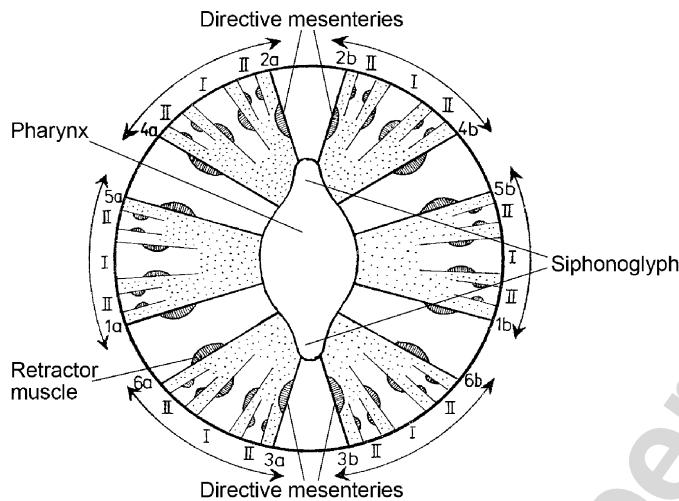


Fig. 3. Cross-section of an Actiniaria polyp at the level of the pharynx. The arabic numbers indicate the sequence of mesentery formation (compare with Fig. 2). The darkened fields represent the retractors at the mesenteries. The dotted fields represent the exocoels. The 6 exocoels of the 12-mesentery state are indicated by arrows. An exocoel is a gastric pouch in which new pairs of mesenteries continuously form (indicated by roman numbers). The resultant new pouches are termed endocoels. They do not give rise to further pouches. White fields represent two types of endocoels. Both do not give rise to further pouches. One type, positioned at the most dorsal and ventral site, is lined by so-called directive mesenteries. The pharynx ectoderm related to these pouches develops a siphonoglyph (after Kästner, 1984, p. 245).

2. Results

2.1. The model: subdivision of the endoderm into compartments

In Anthozoa, I propose, there are three endodermal compartments, based on the observation that in several groups three types of gastric pouches can be distinguished (as noted earlier). I assume that the 6 exocoels and the respective part of the mesenteries are made by a subtype of endodermal epithelial cells termed Endo A cells, the four nondirective endocoels are formed by Endo B cells, and the two pouches that are lined by directive mesenteries are formed by Endo C cells.

This concept is applied to mesentery formation of various taxonomic groups (Figs. 2 and 6). Initially the endoderm is uniform and may consist of Endo A cells only. Then, successively, groups of cells change their state and because of that change, form new compartments. A new compartment forms within the center of an existing one. For instance, a new Endo B compartment forms within an Endo A compartment, causing the formation of two new borders between A and B. It turns out that only a few alternative sequences can be constructed (Fig. 6). In some taxonomic groups all three types of gastric pouches can be

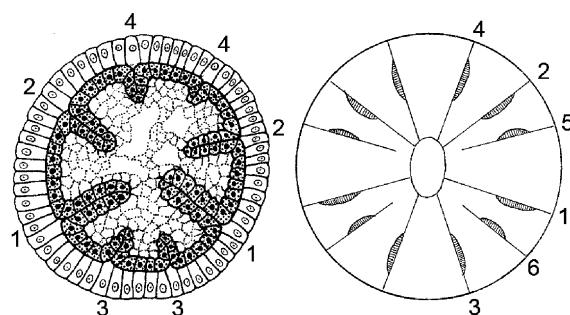


Fig. 4. Cross-section of *Bolocera turdiae* (Actiniaria) and a typical member of Madreporaria. Left and middle: two steps in the postembryonic development in *Bolocera turdiae* (Actiniaria), median sections. The numbers indicate the sequence of mesentery formation. Note that in the course of mesentery formation, the number of cells in the circumference does not increase much. The sequence of mesentery formation is not typical for Actiniaria (see Fig. 3) but is typical for Madreporaria (from Mergner, 1971, after Gemmil, 1922). Right: a typical 12-mesentery state of Madreporaria (from Kästner, 1984, p. 260).

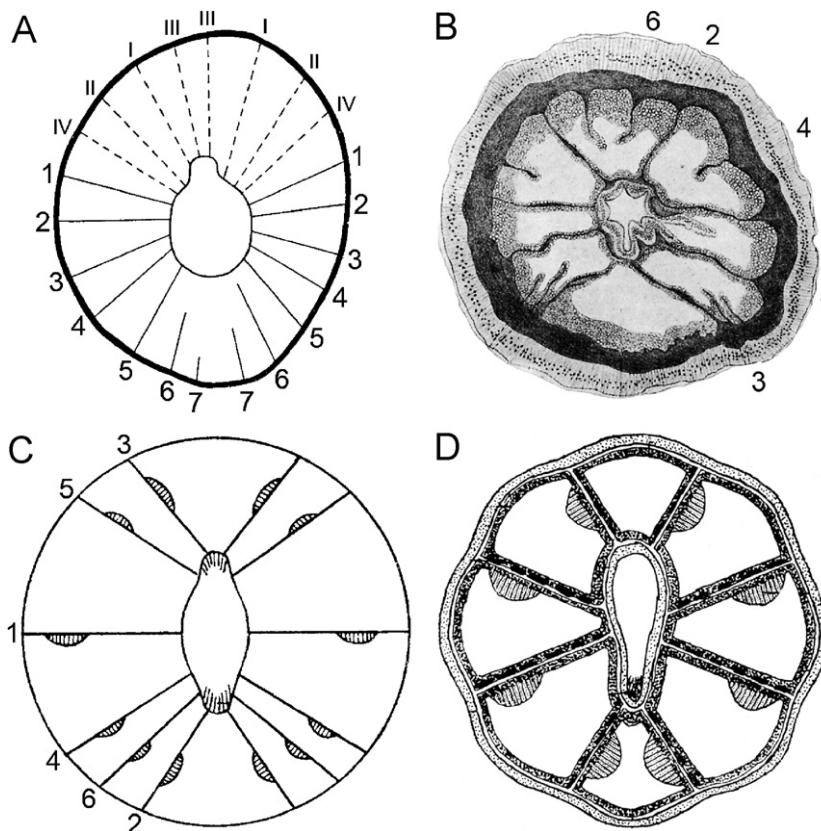


Fig. 5. Mesentery formation in various Anthozoa. (A) Ceriantharia. The first (proto)mesenteries are indicated by roman numbers in the sequence of their appearance, and those which follow (metamesenteries) are indicated by arabic numbers. At the dorsal side one pair of directive mesenteries has formed (mesentery pair III). New pairs of mesenteries form exclusively in the most ventral pouch (pair 7 has just formed) (from Pax, 1914, after McMurrich, 1910). (B) Zoantharia. Transversal section through *Isozoanthus giganteus* displaying 12 protomesenteries and 4 metamesenteries (two pairs close to mesentery pair 3). The most ventral side is occupied by a pair of perfect directive mesenteries (mesentery pair 3). At the dorsal side is a pair of imperfect directive mesenteries (mesentery pair 6). New mesenteries form exclusively in the pouches (exocoel) right and left to the ventral directive pouch. In each of the exocoels a pair of metamesenteries has just formed (from Pax, 1925, after Carlgren, 1906). (C) Scheme of mesentery formation in Antipatharia. The dorsal and ventral positions are occupied by pairs of directive mesenteries (from Kästner, 1984, p. 280). (D) Cross-section through a polyp of Octocorallia (from Kästner, 1984, p. 284). Usually, mesenteries form almost synchronously.

distinguished in “the 12-mesentery state.” For the others a similar 12-mesentery state is assumed to have been reached (see Figs. 4 and 5). Octocorallia (see Fig. 5) are omitted from the scheme (Fig. 6). They form their mesenteries more or less synchronously. I could not find a group-specific sequence of compartment formation in the literature, but the final state easily fits the concept of compartments existing in the endoderm.

The following conclusions can be drawn: (1) Endodermal cells change their state repeatedly. In some taxonomic groups and at certain positions in the polyp, this takes place during the whole life of the polyp. (2) In the first step of mesentery formation, in all groups, some Endo A cells change to the Endo B state but in no case to the Endo C state. (3) In the second step, either an Endo C (Actiniaria, Antipatharia) or an Endo B compartment is formed. A new compartment forms in the center of an existing one. (4) In the third step, some cells change to the Endo C state in all groups and in all cases this takes place in the center of an existing compartment. Thereafter, only Madreporaria and Zoantharia produce a further Endo C compartment. (5)

The plane of symmetry (sagittal axis) runs through the Endo C compartments. It thus can be argued that the Endo C compartments are involved in controlling the bilateral symmetric sequence of compartment formation. (6) In most taxonomic groups, Endo A compartments seem to flank the Endo C compartments of polyps of the 12-mesentery state.

2.2. Mechanism of compartment formation

For the generation of structures in neighboring positions, Meinhardt and Gierer (1980) and Meinhardt (1982) proposed a mechanism based, first, on mutual activation of locally exclusive cell states called lateral activation. The assumptions made are that each of the two cell states is controlled by a specific activator that stabilizes that state. Second, cells of each state produce a diffusible substance that cells of the other state need to maintain their own state. Third, a common repressor brings about the local mutual exclusion of the two states. The reason for a new compartment B to form in the center of compartment A on

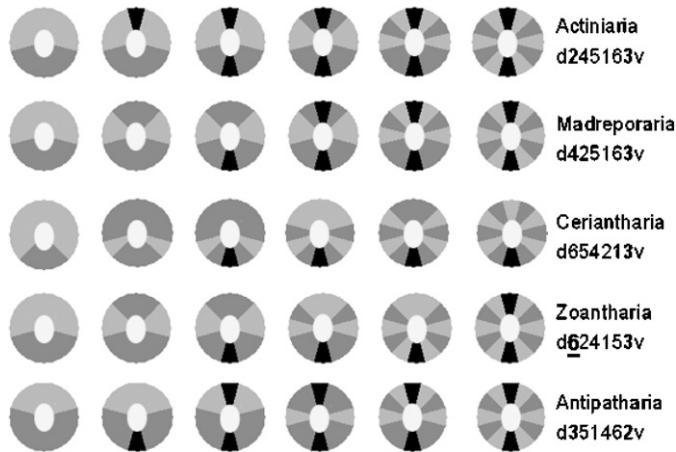


Fig. 6. Compartment formation in various Anthozoa. Shown are schemes of transversal sections through developing polyps. Light gray, Endo A compartment; deep gray, Endo B compartment; black, Endo C compartment. Left: initially the uniform endoderm (Endo A) is subdivided into two pouches made of Endo A and Endo B cells, respectively. This results in the formation of a pair of mesenteries (see Fig. 2). From left to right: the sequence of mesentery formation in various taxonomic groups. The numbers at the 12-mesentery polyps indicate the temporal sequence of mesentery formation from dorsal (d) to ventral (v). Directive mesenteries are represented by boldface numbers. In addition, the dorsal imperfect pair of mesenteries in Zoantharia is underlined. Note that in each step, two mesenteries form symmetrically to the right and to the left of a sagittal plane. The last two steps may occur synchronously. The last step, the formation of the last two pairs of mesenteries, generally causes an Endo A compartment (exocoel) to be in contact with an Endo C compartment. Members of all groups may reach a stage with a similar spatial pattern of compartments. Compartment size is arbitrary.

growth is that the cells in the center of compartment A cannot be reached any more by the diffusible substances generated by B-cells, right and left of compartment A, which cells of A need to maintain their own state. When the cells of compartment A form a stripe from the apical to basal body end, then cells of compartment B will also develop in the form of a stripe in the center of compartment A. To allow computer simulations of the patterning processes, the terms “activator,” “repressor,” and “diffusible substance that provides mutual aid” summarize chains of interacting substances including receptors into single, manipulable sets with defined properties. In the following, the term “lateral activation” is used as a generic term. Berking and Herrmann (in press) propose that this mechanism controls the formation of two endodermal compartments in Scyphozoa. The subtype of the lateral activation mechanism applied to explain compartment formation in Scyphozoa is a mutual dependence: One compartment cannot exist without the other.

Attempts to simulate the patterning in Anthozoa by assuming three states and a mechanism of mutual dependence were not successful. It is possible to generate the pattern of the first six compartments appropriately by computer simulations, but not the following compartment patterns (not shown). In particular, new compartments do not form in the center of existing ones, as observed in

Anthozoa, but rather at the border between two compartments: The system properties of the mutual dependence mechanism cause the two existing compartments to favor the formation of the third one at their common border.

A much better fit with the observations is achieved by assuming that only two compartments (Endo A and Endo B) are generated by mutual dependence, as proposed for Scyphozoa (Eqs. (1), (2), (5a), and (6a)). The activators g_a and g_b are the (autocatalytic) substances required for stabilization (Eqs. (1) and (2)). A common repressor brings about the local mutual exclusion of the two states Endo A and B (Eq. (4)). The diffusible substances s_a and s_b provide far-reaching aid from one feedback system to the other (Eqs. (5a) and (6a)). The compounds interact with the opposite feedback loop in such a way that a mutual dependence of the states results, for instance; in the absence of s_b the g_a production ceases (Eq. (1)). In contrast the third compartment, Endo C, is assumed to be generated by a mechanism of “autocatalysis and lateral inhibition” (Gierer and Meinhardt, 1972) (Eqs. (3a) and (7)). The substance s_c (Eq. (7)) inhibits the autocatalytic production of g_c (Eq. (3a)). The equations are suited for simulations in a row of cells. How the stripes of Endo A and B can form oriented along the apical–basal axis, and how an Endo C compartment can develop in the form of a stripe, are discussed in a separate section

$$\frac{\partial g_a}{\partial t} = \frac{\alpha s_b g_a^2}{r} - \beta g_a + D_{ga} \frac{\partial^2 g_a}{\partial x^2} + \rho_1, \quad (1)$$

$$\frac{\partial g_b}{\partial t} = \frac{\alpha s_a g_b^2}{r} - \beta g_b + D_{gb} \frac{\partial^2 g_b}{\partial x^2} + \rho_1, \quad (2)$$

$$\frac{\partial g_c}{\partial t} = \frac{\delta g_c^2(g_a^2 + g_b^2)}{s_c} - \gamma g_c + D_{gc} \frac{\partial^2 g_c}{\partial x^2} + \rho_2, \quad (3a)$$

$$\frac{\partial r}{\partial t} = \alpha s_a g_b^2 + \alpha s_b g_a^2 - \varepsilon r, \quad (4)$$

$$\frac{\partial s_a}{\partial t} = \varsigma g_a + \eta g_c - \phi s_a + D_{sa} \frac{\partial^2 s_a}{\partial x^2}, \quad (5a)$$

$$\frac{\partial s_b}{\partial t} = \varsigma g_b + \varphi g_c - \kappa s_b + D_{sb} \frac{\partial^2 s_b}{\partial x^2}, \quad (6a)$$

$$\frac{\partial s_c}{\partial t} = \lambda g_c^2(g_a^2 + g_b^2) - \mu s_c + D_{sc} \frac{\partial^2 s_c}{\partial x^2}. \quad (7)$$

Fig. 2 (lower row) shows a simulation of early steps of compartment formation in Actiniaria. Initially, the endoderm of the larva consists of undecided cells. In all cells the concentration of g_a is identical and higher than of g_b due to a higher removal rate of s_a than of s_b . In Actiniaria, the first subdivision of the gastric cavity usually results in two compartments of different size (Fig. 4). Accordingly, in the simulation the Endo B compartment is smaller than the Endo A compartment because of the (mentioned) higher removal rate of s_a than of s_b . A subdivision of the uniform field into compartments takes place when the range of the

diffusible substances becomes smaller than the size of the field of cells. Either the size of the field of cells increases by an increase of the number of cells, and/or the range (extent of influence) of the diffusible substances decreases. In the course of early mesentery formation, the animal does not grow very much (Fig. 4). It thus appears that early in development, the range of the diffusible substances in the tissue decreases. The simulation has been performed by successively reducing the diffusion constants.

In this approach, the activator g_c is generated in the presence of high concentrations of either g_a or g_b . Approaches in which g_c locally excludes the production of g_a and g_b turn out to be inappropriate. They fail to reproduce the observed sequence of compartment formation; in particular, they cause Endo C compartments to form at the border between Endo A and Endo B.

2.3. Directive mesenteries and the bilateral symmetry of polyps

In general, polyps of Actiniaria display a bilateral symmetry but deviations thereof are not rare. There are specimens of various species that lack directive mesenteries and a siphonoglyph, whereas other specimens of the same species have two or even more. The former display a radial symmetry. In various Actiniaria species with six regularly spaced siphonoglyphs can occasionally be observed. *Gyrostoma herdwigi* usually has six siphonoglyphs (Fig. 7) (Kwietniewski, 1898) but rarely three (Carlgren, 1900, cited in Pax, 1914). Members of other species display an asymmetric arrangement of siphonoglyphs (Fig. 7). Neither a bilateral symmetry, nor the existence of a pair of directive mesenteries and a siphonoglyph, is necessary for survival. It appears that the bilateral symmetry is simply the most frequent symmetry that may have a particular selective advantage for the animal.

According to the model, within the circumference an alternation of the compartments Endo A and Endo B is

inevitable. One possibility to achieve a correct localization of the three compartments in relation to each other is that (1) the production of activator g_c depends on the presence of high levels of either g_a or g_b (Eq. (3a)) and (2) that g_c has a slightly different influence on the production of the substances s_a and s_b , respectively (Eqs. (5a) and (6a)). This can cause a bilateral symmetric sequence of Endo A and Endo B formation, with Endo C at the dorsal and ventral position in the center of an Endo A. Deviations from the bilateral symmetry such as 6 or 3 (almost) regularly spaced Endo C compartments at short distances from each other may result from an unusually low lateral inhibition (via s_c) between Endo C compartments. An alternative explanation may be that there is a time window within which Endo C compartments can form. Outside this window the basic production of g_c may be too low and/or the basic production of s_c may be too high to allow the initiation of a self-amplified g_c production. When the window remains open for a longer time, more Endo C compartments than usual may form. The latter explanation accounts better than the first for the finding of polyps without Endo C compartments as well as for the absence of Endo C compartments in the course of polyp growth after the first two have formed.

2.4. Lateral inhibition between Endo C compartments by means of an inhibitor or by depletion of a substance necessary for activation?

In natural populations of *Metridium marginatum*, polyps with 1–3 siphonoglyphs have been found. In polyps of this species, in the course of regenerating complete polyps from tissue fragments (artificially obtained by sectioning or naturally by a certain type of asexual reproduction), a pair of directive mesenteries usually forms at the site of the former wound (Hahn, 1905). This can result in mono-, di-, and triglyph polyps, depending on the number of siphonoglyphs initially present in the fragment. The

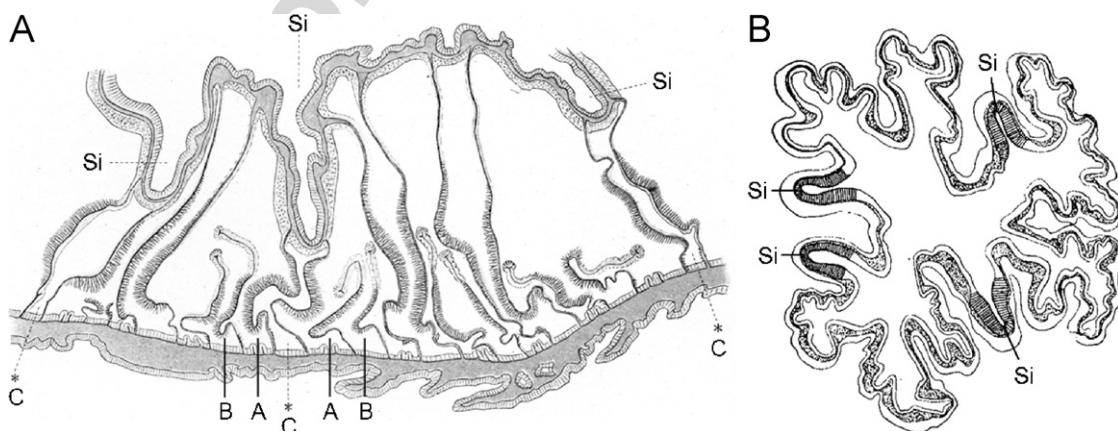


Fig. 7. Specimen with more than two siphonoglyphs. Left: section through *Gyrostoma herdwigi* one third from the apical end showing about one half of the body wall, including three of the six pairs of directive mesenteries and three of the six siphonoglyphs (Si) of the specimen (from Kwietniewski, 1898). Center: proposed endodermal compartments are indicated by A, B, and C. Right: cross-section through the heavily folded pharynx of a specimen of *Rivetia papillosa* displaying the asymmetrical arrangement of four siphonoglyphs (Si, darker bits within folds) (from Pax, 1914).

siphonoglyphs are not regularly spaced. However, in all cases exocoels and endocoels appear to alternate regularly in the circumference.

The cause for the formation of additional siphonoglyphs in the regeneration of polyps from tissue fragments may be a loss of substances from the tissue at the wound, including a loss of s_c . A loss of s_c allows g_c to feed back positively on its own production (Eq. (3a)), which results in the formation of an Endo C compartment at the site of the former wound. Activation as a result of loss of signaling compounds strongly indicates an activator–inhibitor system. A necessary condition is that the diffusion constant of the activator must be smaller than that of its antagonist. It is obvious that a low inhibitor level can allow autocatalysis. The alternative, an activator-depleted substrate system (Gierer and Meinhardt, 1972) cannot account for the observed regeneration. In such a system the self-enhanced production of the activator depends on a substrate that is produced everywhere. In the course of activator production, this substrate is used up. Inhibition between regions of enhanced activator production thus results from the depletion of this substrate in the surroundings of the activator-producing cells. Clearly, a loss of this substrate cannot stimulate the autocatalytic production of the activator. Taken together, these observations support the activator–inhibitor model.

The sequence of compartment formation in the other taxonomic groups such as Madreporaria, Antipatharia, Zoantharia, and Ceriantharia (see Figs. 4–6) can be simulated with the same set of equations by making small changes in the parameters, including the basic production and the removal rate of the compounds that are involved in the formation of the three compartments (not shown).

2.5. Endodermal compartments form in stripes

The simulation of the lateral activation equations in two dimensions leads to stripes (Meinhardt, 1982). The reason is that a stripe-like arrangement of the two cell types allows the most efficient mutual stabilization. To organize mesenteries, these stripes must develop in an apical/basal orientation. There are several ways to orient the stripes. Shoji et al. (2003) found that a diffusion anisotropy is effective at specifying the direction of stripes formed by a reaction–diffusion system. Berking and Herrmann (in press) have shown that a feedback of the polar organization of the polyp can lead to stripes in the desired orientation. The tissue polarity may be controlled by a gradient of a tissue property termed positional values or sources along the apical–basal axis, as several researchers have proposed it exists in *Hydra* (Wolpert, 1969; Gierer and Meinhardt, 1972; Meinhardt, 1993; Müller, 1995; Berking, 2003, 2006). Simulation in two dimensions results in the apparent formation of Endo A and Endo B stripes if the gradient of positional values (d) influences the production of the substances s_a and s_b

(Eqs. (5b) and (6b))

$$\frac{\partial s_a}{\partial t} = \varsigma \frac{g_a}{d} + \eta g_c - \phi s_a + D_{sa} \frac{\partial^2 s_a}{\partial x^2}, \quad (5b)$$

$$\frac{\partial s_b}{\partial t} = \varsigma \frac{g_b}{d} + \varphi g_c - \kappa s_b + D_{sb} \frac{\partial^2 s_b}{\partial x^2}. \quad (6b)$$

The stripes form parallel to the orientation of the gradient (Fig. 8B, first and second line). In Anthozoa, mesenteries visibly start to form at the apical body end (see below). The parameter d is thus introduced in Eqs. (5b) and (6b) in such a way that Endo A and Endo B stripes start to form at the apical body end, i.e., where the positional value is high. Such stripes even form when the simulation was started by a random fluctuation of the g_a concentration in the field of cells (Fig. 8B, first and second line). Without a gradient of positional values, Endo A and Endo B stripes form in a random orientation. These stripes are often short and branched (Fig. 8A, first and second line).

Stripes are also formed in an activator–inhibitor system, if the production of the activator is limited by saturation (Meinhardt, 1995, 2004). Accordingly, to generate Endo C compartments in the form of stripes the production of g_c should display saturation (Eq. (3b))

$$\frac{\partial g_c}{\partial t} = \frac{\delta g_c^2(g_a^2 + g_b^2)}{s_c(1 + \tau g_c^2(g_a^2 + g_b^2))} - \gamma g_c + D_{gc} \frac{\partial^2 g_c}{\partial x^2} + \rho_2. \quad (3b)$$

Simulation with (3b), (5b), and (6b) instead of (3a), (5a), and (6a), respectively, results in the formation of an Endo C stripe (Fig. 8B, last line). Because of the slightly higher removal rate of s_a compared to s_b , an (unbranched) Endo C stripe forms in the center of an Endo A stripe. In Actiniaria in the 12-mesentery state, Endo C stripes are rare—only two form, flanked by Endo A stripes (Fig. 3). In the simulation, one Endo C stripe forms in the center of an Endo A stripe but not also in the center of the adjacent Endo B and Endo A stripes (Fig. 8B).

Even an established pattern of stripes in random orientation transforms into a regular pattern of stripes in apical–basal orientation when a gradient of positional values is applied (not shown). This demonstrates how strong the influence of the gradient can be and may help us understand the stability of the striped pattern in the course of growth, regeneration, and the various forms of asexual reproduction. For Cnidaria the positional value is generally argued to be a primary element of the pattern-forming system. I thus propose that this parameter, not a diffusion anisotropy, controls stripe formation in Anthozoa.

2.6. Late development: insertion of new compartments in the center of existing compartments

Polyps of several taxonomic groups continue to produce mesenteries after the 12-mesentery state. In Actiniaria and Madreporaria, new mesenteries usually form in pairs in the exocoels, that is, in the center of each Endo A compartment (Figs. 3 and 9). The new pairs house an endocoel that

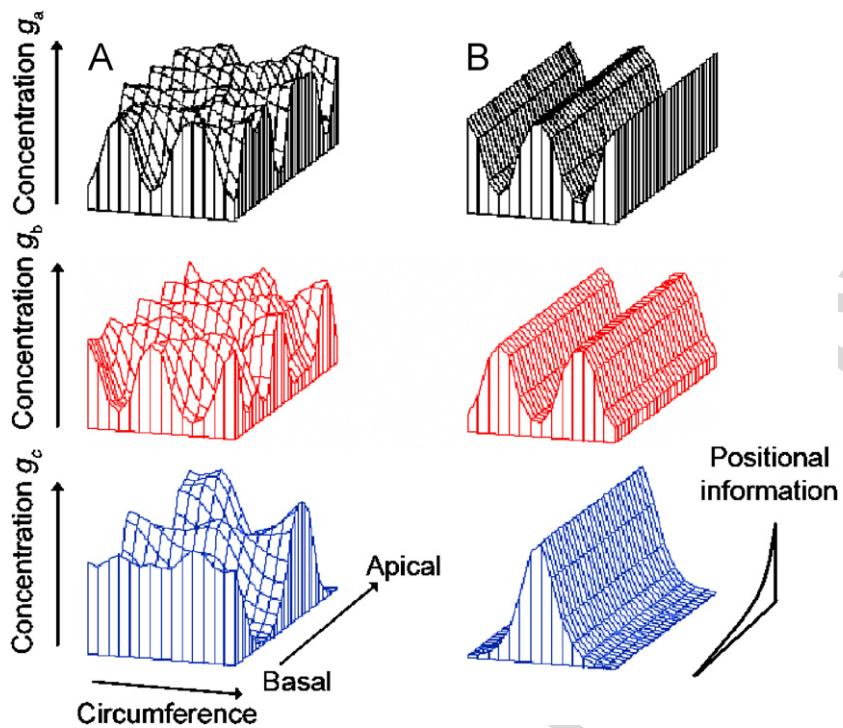


Fig. 8. Formation of compartments in the form of stripes. (A) Simulation of Eqs. (1), (2), (3b), (4), (5b), (6b), and (7) in two dimensions results in a subdivision of a field of cells in stripes of random orientation. Simulation was made without a gradient of positional values ($d = 1$) and $\gamma = 0.02$ instead of $\gamma = 0.03$. For other conditions, see (B). (B) Simulation of equations (1), (2), (3b), (4), (5b), (6b), and (7) in two dimensions results in a subdivision of a field of cells in stripes parallel to the longer axis of the rectangle in which either g_a or g_b and/or g_c , is present in high concentration. The field may represent an animal virtually sectioned from basal to apical. Field size: $x = 15$, $y = 30$ cells. Gradient of positional values from apical (maximal) = 0.01 to basal with a change of $d = 1.1$ per cell. Calculated with the following constants: diffusion constants: $D_{ga} = D_{gb} = 0.01$, $D_{gc} = 0.3$, $D_{sa} = D_{sb} = 0.03$, $D_{sc} = 0.2$, $D_r = 0$; removal rates: $\beta = 0.04$, $\gamma = 0.03$, $\varepsilon = 0.08$, $\phi = 0.031$, $\kappa = 0.03$, $\mu = 0.01$; basic production: $\rho_1 = 0.001$, $\rho_2 = 0.0001$; constants: $\alpha = 0.03$, $\delta = 0.02$, $\zeta = 0.01$, $\lambda = 0.012$, $\eta = \varphi = 0$, $d = 1.1$, $\tau = 0.8$. Starting at several random positions of elevated g_a concentration, stripes of Endo A and Endo B cells finally form that run from the apical to the basal body end, causing the formation of gastric pouches separated by septa. An Endo C stripe formed in the center of an Endo A stripe. The technical basis of this simulation has been developed by Meinhardt (1995).

is, according to the model, an Endo B compartment. Endo B compartments grow to a certain size and then stop growing, whereas the two Endo A on the right and left continue to grow and give rise to further Endo B stripes (Fig. 3). Apparently, a compartment-specific growth control exists.

Within a compartment, cell proliferation may continue as long as a certain cell parameter exceeds a certain threshold value. The requested parameter should be large only in a small compartment. Because of the differences in the diffusion constants, such a parameter is the concentration ratio g_i/s_i ($i = a, b$, or c) (see Fig. 9): The substance g_i may stimulate cell proliferation, whereas s_i antagonizes it. Note that s_i , directly or indirectly, has two functions: (1) It provides mutual activation (s_a and s_b) and lateral inhibition (s_c), respectively, in compartment formation, and (2) it acts in growth control within a compartment. The Endo B compartment grows until the concentration ratio g_b/s_b has fallen to a certain threshold value. Proliferation may then cease. The Endo A compartment behaves differently. In its center the production of g_b is triggered before proliferation stops. This causes Endo A compartments to produce Endo B compartments in an “endless” sequence.

The model proposed also accounts for the most complex type of compartment formation (Fig. 9, compare with Fig. 3): Endo B compartments form within an Endo A compartment right and left of an Endo C compartment. In this case, the new compartments do not form in the center of the Endo A compartment (which coincides with the center of the Endo C compartment) but, rather, form in a symmetrical manner in the periphery of the Endo A compartment.

Although in Actiniaria and Madreporaria, this type of compartment formation is one of several ways (Figs. 3 and 4), in Zoantharia it is the only one observed (Fig. 5). Note that the new Endo B compartments form very close to the ventral Endo C compartment. After being formed, these new pairs of mesenteries become displaced by cell proliferation. Then new Endo B compartments form to the right and left of the Endo C compartment, and so on. Thus signals deriving from the Endo C compartment apparently allow growth in the adjacent Endo A compartment. One possibility is that s_c directly interferes with growth control in the Endo A compartment: s_c antagonizes the growth inhibition by s_a . Thus growth may be controlled by $g_a/(s_a/s_c)$.

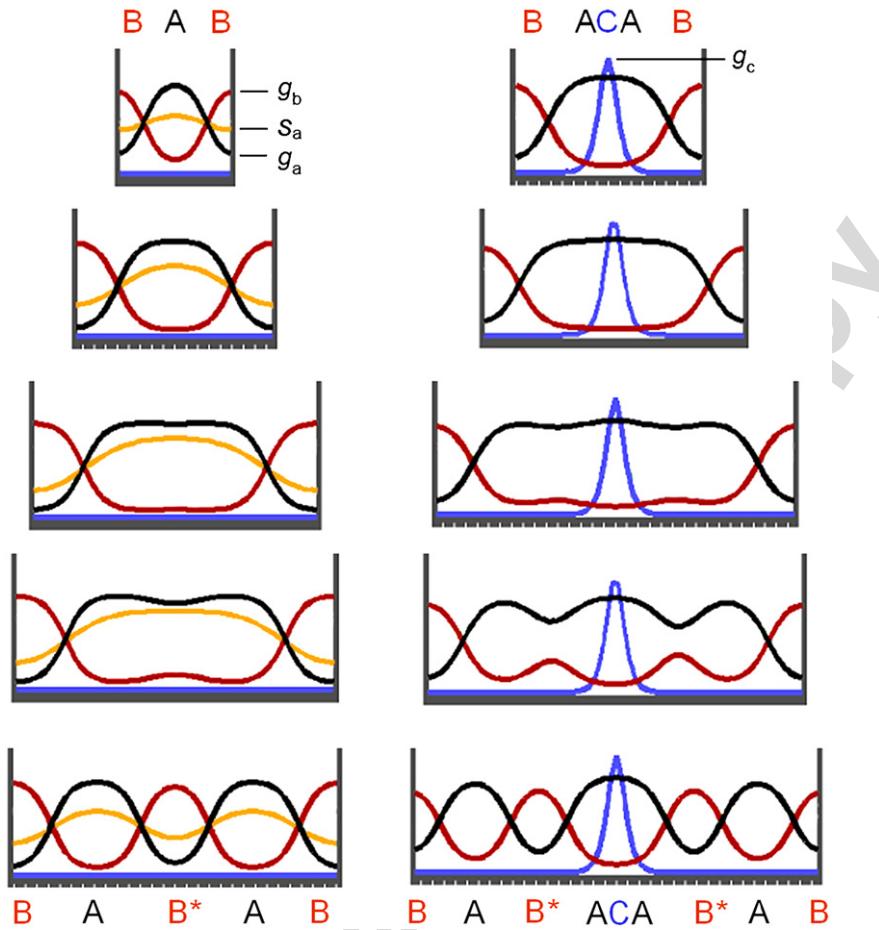


Fig. 9. Mesentery formation in exocoels. Shown is the concentration pattern of the activators g_a (black), g_b (red), and g_c (blue), and of the substance s_a (orange) in a row of cells. The pattern is generated by applying the equations noted. This concentration pattern causes the formation of the compartments: Left column, from top to bottom: compartments Endo B (half compartment), A and B (half). Then growth is simulated by adding cells in the center of the Endo A compartment. This finally results in the formation of a new Endo B compartment (B^*) in the center of the Endo A compartment. Right column, from top to bottom: if an Endo C compartment is in the center of an Endo A compartment, growth leads to the formation of two Endo B compartments, one right and one left of the center of the Endo A compartment. Left column: the generation of g_c is prevented by $\rho_2 = 0$ (basic production) and $\delta = 0$ (production constant). Other parameters: $D_{ga} = D_{gb} = 0.03$, $D_{gc} = 0.01$, $D_{sa} = D_{sb} = 0.2$, $D_{sc} = 0.4$. Removal rates: $\beta = 0.01$, $\gamma = 0.01$, $\varepsilon = 0.02$, $\phi = 0.011$, $\kappa = 0.01$, $\mu = 0.01$; basic production: $\rho_1 = 0.001$; constants: $\alpha = 0.01$, $\zeta = 0.01$, $\lambda = 0.03$, $\eta = 0.04$, $\varphi = 2$. Conditions for first graph: 19 cells. Right column: parameters in the right column are as for left column, except for the following: $\rho_2 = 0.0001$, $\delta = 0.02$ (the generation of g_c is allowed). Conditions for first graph: 19 cells, $\varphi = 1$.

In Ceriantharia, new pairs of mesenteries form opposite to the single Endo C compartment (Fig. 5). In the center of a just-formed Endo A or an Endo B compartment—the opposite type of compartment forms, and so on. A simple explanation would be that a signaling compound generated by the Endo C compartment, such as s_c , acts as co-inhibitor in controlling the growth of Endo A and Endo B compartments. Growth may be controlled by $g_a/(s_a + s_c)$ and $g_b/(s_b + s_c)$, respectively.

2.7. Compartments in the ectoderm

In Anthozoa polyps, three body parts are usually distinguished along the apical–basal axis: the basal disc, the body wall, and the oral disc, including the pharynx. The respective ectodermal epithelia differ from each other.

Several species have a sharp border, called the limbus, between the basal disc and the body wall. In some species (such as *Actinia equina*), this border forms a colored belt. The border between body ectoderm and oral disc ectoderm often forms a fold, termed the margo or parapet. Given these observations, I propose that the polyp's ectoderm is subdivided into (at least) three zones, which have features of compartments. However, in several species the tissue between parapet and pharynx displays such a rich pattern that more than three ectodermal compartments may exist in Anthozoa.

Models for pattern control in *Hydra* suggest mechanisms that enable a subdivision perpendicular to the apical–basal axis of the body. Along this axis a gradient of positional values or sources is proposed to exist (Wolpert, 1969; Gierer and Meinhardt, 1972; Meinhardt, 1993; Müller,

1995; Berking, 2003, 2006). A certain range of positional values may cause the formation of a certain ectodermal compartment. The role of lateral activation in these subdivisions remains to be studied.

The proposed existence of ectodermal compartments helps explain the formation of siphonoglyphs and mesenteries: A siphonoglyph (ectoderm) is always associated with a pair of directive mesenteries (endoderm). In various species of Actiniaria additional pairs of directive mesenteries form, and they too are associated with a siphonoglyph (Fig. 7). In Zoantharia, when the ventral directive mesenteries reach the end of the pharynx a siphonoglyph forms there. The dorsal directive mesenteries are not in contact with the ectoderm of the pharynx, and hence a siphonoglyph does not form there. These observations indicate that the Endo C compartment apparently induces siphonoglyph formation in cells of the pharynx ectoderm compartment. The contact appears necessary and sufficient for siphonoglyph formation. Obviously, body ectoderm cannot respond in that way; it appears incompetent to do so. This difference in response may support the proposition that the ectoderm is subdivided into compartments.

2.8. Are there two different types of Endo C compartments?

Octocorallia produce two pairs of directive mesenteries, but a siphonoglyph forms only in the ventral position (Fig. 5). The respective dorsal tissue differs from other tissues in the vicinity and differs from that of the siphonoglyph. In Octocorallia, possibly two different compartments C exist, controlled by g_c and g'_c , respectively. Only one of them can induce a siphonoglyph. The activators g_c and g'_c mutually exclude each other locally. This can result from a cross-reaction of s_c in the opposite system (g'_c and s'_c) and vice versa, that is, s'_c in the system (g_c and s_c). Thus the compartments Endo C and C' may also represent a system of lateral activation. However, in contrast to the compartments Endo A and B, which depend on each other in formation and existence, the compartments Endo C and C' can form and survive in the absence of the opposite one. This type of mutual aid is a (weak) mutual support.

In several Actiniaria, the dorsal and the ventral siphonoglyphs are not of identical size. Further, members of the Edwardsiidae display two pairs of directive mesenteries, but either only one siphonoglyph is formed or none (Pax, 1914) suggesting that also in Actiniaria two different Endo C compartments exist.

2.9. Perfect and imperfect mesenteries

There are two types of mesenteries, perfect and imperfect ones (Figs. 1 and 5). Perfect mesenteries reach from the basal end of the pharynx to the basal body end. Imperfect ones almost reach from the mouth to the basal body end. The formation of perfect mesenteries is initiated at the mouth and spreads down both the body column and the

pharynx (Appellöf, 1900, cited in Pax, 1914). I thus propose that mesentery formation starts in the endoderm at a position where the two ectodermal compartments meet. When mesentery formation spreads in both directions, a perfect mesentery forms. When it only spreads down the body column, an imperfect mesentery forms. There are two possibilities: (1) Either a mesentery remains imperfect because the respective endodermal compartment does not line the pharynx, (2) or the endodermal compartment lines the pharynx ectoderm, but nevertheless a mesentery does not form. Siphonoglyph formation in Zoantharia provides arguments for the first possibility: In Zoantharia a siphonoglyph is associated with the ventral perfect pair of directive mesenteries but not with the dorsal imperfect pair. Possibly the dorsal Endo C compartment does not reach the pharynx ectoderm. The respective endodermal tissue may consist of Endo A cells (Fig. 5). However, other observations are more in favor of the second explanation: In Zoantharia, only the first pairs of mesenteries are perfect. Then additional mesenteries form in pairs, wherein usually one member of the pair is perfect and the other one is imperfect (Fig. 5). In this case the model predicts that the endodermal compartment will reach the end of the pharynx, although a mesentery is formed only on one of the two compartment borders. No good explanation exists for the absence of a mesentery at the other border. Perhaps there is not enough material for two mesenteries to form in close proximity, or perhaps the pharynx ectoderm supplies the endoderm with a compound necessary for mesentery formation in limited amounts, as has been discussed for Scyphozoa (Berking and Herrmann, in press). An observation of compartment-specific gene expression may decide this question. At present, researchers have found several genes, including *Hox* and *Dpp* (Finnerty et al., 2004; Matus et al., 2006), that are asymmetrically expressed during development. However, a compartment-specific gene expression in the endoderm does not seem to have been found yet.

2.10. Positioning of the retractor muscle in mesenteries

In adult polyps, mesenteries are no longer simple folds of endodermal tissue. As is well known from textbooks, the free, inner edge of a mesentery displays a rich differentiation, which I will not discuss here, and in members of most groups the two sides are asymmetrically equipped with muscles. At one side, a muscle runs longitudinally from the oral to the aboral body end, forming a retractor. On the other side, the muscle is perpendicularly oriented. In Actiniaria and Madreporaria, the retractor usually forms at the Endo B side of a mesentery, and in the case of an Endo A–Endo C contact, it forms at the Endo A side. However, exceptions occur. In *Anemonia sulcate* (Actiniaria), Simon (1892, cited in Pax, 1914) found several mesenteries with the retractor oriented to the exocoel. In Octocorallia all retractors point to the ventral side (Fig. 5). In Antipatharia, van Pesch (1914, cited in Pax, 1940)

distinguished 10 different types of orientation of retractors, including types that have a retractor at the inner side of the directive mesenteries. At present, only one strict rule seems obeyed: If a retractor is differentiated, the retractor is located on one side of a mesentery. The development of a retractor is apparently controlled by a combination of the local compartment specificity, and a far-reaching influence deriving from the dorsal and/or ventral compartment (Endo C).

3. Discussion

In this article, I propose that the bilateral organization of Anthozoa polyps is controlled by a combination of two mechanisms: “lateral activation” (Meinhardt and Gierer, 1980; Meinhardt, 1982) and “autocatalysis and lateral inhibition” (Gierer and Meinhardt, 1972). These combined mechanisms successively subdivide the endoderm into stripes (compartments) that run from the apical body end to the basal body end. Three different compartments exist, and where two different ones meet they form a mesentery. The term *compartment* is used because these tissues share properties with the tissues termed compartments in other organisms. Cells of a compartment form a continuous sheet. In general, after cell division the state of the compartment is maintained in the descendants. However, under certain conditions a group of cells can switch into a different state.

Some authors place Anthozoa at the evolutionary base of the Cnidaria (for example, see Martindale, 2005). One argument for this placement is that the members of all other taxonomic groups produce medusae. Other authors argue that all recent Cnidaria originate from a fertile actinula differing from the modern actinula larva only in its ability to reproduce itself. With the evolution of a quadrant stomach, all the essential features for the evolution of all four classes of Cnidaria would have been present (Korschelt and Heider, 1890; Heider, 1914; Marcus, 1958; Rees, 1966, for review, see Bouillon, 1993a, 1993b). Thiel (1966) and Hand (1966) argue that a scyphozoan-polyp-like individual with four septa was the forerunner of both Scyphozoa and Anthozoa. The data presented here seem to support this view. The two compartments (Endo A and Endo B) of the hypothetical tetraradial actinula and the Scyphozoa polyp are produced by a mechanism of lateral activation that includes a mutual dependence of cell states that mutually exclude each other locally. This system property causes the formation of these compartments in an alternating sequence in the circumference of the polyp. Scyphozoa polyps generally have four endodermal compartments, two of each type, those of Anthozoa, generally more. The “innovation” of Anthozoa is an additional type of compartment (Endo C). That compartment leads to the directive mesenteries and the siphonoglyph. I propose that the formation of the Endo C compartment is controlled by a mechanism of autocatalysis and lateral inhibition, that is, a mechanism that combines a local self-amplification of

activator production with the inhibition of that production in the surroundings. An interaction between the two pattern-forming systems causes the Endo C compartment to form in the center of one of the “old,” already existing compartment (Endo A or B). Therewith the mesentery pattern of the hypothetical actinula-like ancestor transforms into that of the Edwardsia stage of present-day Actinia. Endo C compartments can exist in variable number, and can even be absent—as observed in members of one and the same species. The system property of autocatalysis and lateral inhibition causes compartments of this type—if they form at all—to keep a certain distance from each other. Because of this property, these compartments change the radial symmetry of the polyp into the usual bilateral one. Patterning via lateral inhibition takes place early in polyp development, usually in the larval state. There appears to be a time window in the early growth period of the animal within which Endo C compartments can form. The range of inhibition, together with the temporal size of this window, largely determines the symmetry of the polyp. In natural populations, the bilateral symmetry may prevail because it has a selective advantage for the animal, possibly by allowing an appropriate flow of water in and out of the gastric cavity. Selection may have favored a certain range of inhibition and a certain size of the time window, but one must keep in mind that animals with zero or many more than two siphonoglyphs do survive under natural conditions.

Some indications suggest that not one but rather two slightly different Endo C compartments exist in one and the same animal of certain species. One of these compartments induces a siphonoglyph; the other either does not or it induces a reduced one. The observations and experimental data appear best explained by assuming that these compartments also form a system of lateral activation. Thus an “ancient” (older than several million years) system of mutual dependence causes the two basic compartments Endo A and B to form, and a “newly invented” (several million years old) system of mutual support in addition causes the formation of the Anthozoa-specific compartments (Endo C and C') that are associated with the directive mesenteries.

In the early phase of polyp development, small quantitative differences in parameters such as diffusion rate, removal rate, and basic production are able to generate the different patterns of mesentery formation observed in Anthozoa. Several details of the patterning processes are still unclear, in particular because we cannot yet distinguish the three compartments in all taxonomic groups, although indications for three different compartments can be found in all groups. In several species the tentacles display a pouch-specific size, color, and form, and their time of appearance and their speed of growth are often pouch-specific (for review, see Pax, 1914, 1925; Doumenc and van Praet, 1987). The compartments can be expected to display a specific expression pattern. Matus et al. (2006) found in early developmental stages of the

Actiniaria *Nematostella vectensis* various genes to be asymmetrically expressed, including *NVChordin*, *NvDpp*, *NvGooscoide*, *NvNetrin*, *NvNoggin*. The analysis was done at such an early developmental stage that it is difficult to decide whether or not the expression domains coincide with the compartments I propose in this paper. However, in a scheme, that summarizes the results obtained (Matus et al., 2006, p. 11199), the border between the expression domains of genes in no case ends at a free edge of a mesentery. That means the expression domains are either smaller or larger than a compartment as proposed here. Matus and coworkers are interested in molecular evidence for deep evolutionary roots of bilaterality in animal development. However, whether or not bilaterality once was “invented” in the forerunner of the present Anthozoa and Bilateria is still an open question. The analysis of differential gene expression in the body wall will certainly contribute to the answer, but we must keep in mind that Bilateria depend on a bilateral organization, whereas Anthozoa apparently do not.

In the late phase of polyp development, the spatial pattern of mesentery formation displays strong group-specific differences. These differences appear to be caused by differences in growth control. Growth within the circumference—the mesenteries are arranged in the “circumference” of the tube—is not uniform. In the endoderm, growth is largely restricted to certain endodermal compartments. The respective ectoderm is forced to follow. It appears that growth is not controlled autonomously by cells of the compartment to which they belong: Compartments in the neighborhood also exert an influence. In particular, the compartment that is lined by the directive mesenteries (Endo C) appears to deliver either a co-inhibitor of the compartment-specific growth inhibitor (in Ceriantharia) or an antagonist of this inhibitor (in Zoantharia).

Until now, in Cnidaria, the term *induction* has been used to explain a certain response of a tissue following a certain transplantation; for example, a complete head forms out of the body wall after the researcher transplants a piece of head tissue into that very position. In such an experiment, both the transplant and the host tissue consist of ectoderm and endoderm. A natural process of induction—such as, in amphibians, the formation of a lens from (competent) ectoderm because of contact with the developing eye cup—has not yet been traced in Cnidaria. Here I suggest that siphonoglyph formation is such a process: Cells of a certain endodermal compartment (Endo C) induce cells of a certain ectodermal compartment (pharynx ectoderm) to differentiate as a siphonoglyph (band of cilia). A siphonoglyph forms only at the position where the inducing and the competent compartments meet. Interestingly, the spindle-shaped larvae of the genus *Zoanthella* (Order: Zoantharia) produce a heavily ciliated fringe that extends from the posterior (mouth) to almost the anterior body end. The fringe is made by ectodermal cells at the site of contact to the already existing ventral Endo C compart-

ment (Heath, 1906; Herberts, 1987). The dorsal Endo C compartment is not yet formed. It appears that in these larvae not only the pharynx ectoderm but also the body ectoderm is competent to respond to the inducing influence of the Endo C compartment with the formation of cilia. The ciliated fringe does not reach the larval anterior, which on metamorphosis transforms into the polyp’s basal disc.

Mutual aid appears to be not only “a factor of evolution” (Kropotkin, 1902) but also a factor of embryogenesis: Ectoderm and endoderm are mutually exclusive states. The germ layers depend on each other in formation and, for a certain time, in survival. Their formation can thus be expected to depend on a mechanism that causes the local mutual exclusion of two cell states combined with the mutual dependence of these states. The cells of the two germ layers develop different adhesion properties. These differences in adhesion alone cause, or at least facilitate, the gastrulation movements. When the range of the influence of the signals involved in mutual dependence is large, a coherent sheet of prospective endodermal cells may invaginate or a polar ingression of single cells may take place. When the range is small, a multipolar ingression of single cells that are separated from others that do not ingress, or a delamination, may take place.

After gastrulation, both the ectoderm and the endoderm subdivide into compartments. In the ectoderm of Cnidaria, the borders are perpendicular to those in the endoderm. This arrangement seems controlled by the primary animal vegetal polarity already present in the oocyte and the consequence of that polarity, the gradient of positional values. In Cnidaria this gradient appears to be established well before structures such as mouth, tentacles, and foot form (Berking, 2003, 2006). There has been a debate about how, in Bilateria, stripes can develop early in embryogenesis, in particular, a stripe in the form of a midline (Shoji et al., 2003; Meinhardt, 2004). The mechanism of compartment formation in the endoderm as proposed here may be a contribution to this debate. If a gradient influences a system of lateral activation, stripes form along this gradient. When this mechanism is combined with a mechanism of local activation and lateral inhibition, as proposed here for the formation of the compartments that are lined by directive mesenteries (Endo C), a stripe with a small diameter forms in the center of an existing stripe of different origin (Endo A or B) (see Fig. 9).

Meinhardt (1982) showed that at the sites of lateral contact between compartments, a “co-operation of compartments” is able to further increase the complexity of a body architecture; for example, it causes the generation of essential signals for limb formation in insects and vertebrates. In Anthozoa polyps, such an interaction may lead to the formation of margo and limbus and possibly also to the formation of the complex structures at the free, inner edge of the mesenteries, called the acontia and the mesentery filaments. The polyp’s “head” usually displays a rich pattern, including tentacles in several rings,

pseudo-tentacles, and fosses. The control of the formation of these structures may include a co-operation of compartments, as suggested for tentacle and rhopalia formation in Scyphozoa (Berking and Herrmann, *in press*).

What about a mesoderm in Cnidaria? In Hydrozoa the entocodon is referred to as a true mesoderm layer (Bouillon, 1993a, b; Boero et al., 1998; Seipel and Schmid, 2005). With respect to Scyphozoa and Anthozoa, similar propositions have been put forward (for review, see Seipel and Schmid, 2005). Are Cnidaria diploblastic animals and Bilateria triploblastic? On the basis of the data presented in this article, one can argue that Cnidaria too are made of compartments. Compartments form stepwise in a hierarchical manner. In all members of the animal kingdom, the first compartments formed are similar and thus labeled identically, as ectoderm and endoderm. In the various taxonomic groups, the later formed compartments are increasingly more different from each other. It would be very interesting to find out whether there is a forerunner of the mesoderm in Cnidaria and Ctenophora. However, this question is a subquestion that depends on the answers to more general questions: What differences and similarities govern the control of the successive formation of compartments in the various groups? What role do mutual dependence and mutual support play in compartment formation? What differences and similarities characterize the architecture, cell composition, and function of the various successively formed compartments in the various taxonomic groups? and What characterizes a germ layer?

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