



## Morphogenetic evolution of hydroid colony pattern

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*Key words:* hydroid colony, heterochrony, colony integration, Hydrozoa

### Abstract

A scheme of evolution of hydrozoan colony pattern is proposed based upon the consideration of macro-morphogenesis. Four main processes play decisive roles: (1) hard skeleton formation by soft tissues, (2) changes in duration of the growth phase relative to the transition to differentiation in interdependent zones of growth, (3) ratio in growth rates between adjacent zones of growth within the rudiment, the shoot, or the whole colony, and (4) spatial relationships among growth zones. The main tendency in morphological evolution of the hydroids is an increasing integration of the colony as revealed by increasing complexity of its structure. That is from a temporary colony towards the permanent one with highly organised shoots, as hydranths and branches are localised in a strictly arranged manner. An analysis of diverse data allows one to state that the main morphogenetic mechanism of increasing complexity in the hydroid colony is convergence, then fusion, of adjacent growth zones, a variant of heterochrony.

### Introduction

Most invertebrates belonging to the phylum Cnidaria form colonies, possessing what is now called a modular level of organisation (Chapman, 1981; Jackson & Coates, 1986). Despite there being diverse morphological features among different groups, the structure and organisation of colonies often look very similar. It is now obvious that gross morphology of the colony evolves in parallel in different groups independent from their phylogenetic relations (Sánchez, 2004).

This paper considers the main factors in the morphogenetic evolution of colony pattern using the polyp stage of hydroids, most of which are modular, as the model. By 'morphogenetic evolution' we mean the set of regulatory processes that leads to increasing regularity and complexity of hydroid colony structure, primarily of the shoots. Here we shall focus mainly on the subclass Leptolida (the old terminology), with examples from

several families. But the processes discussed are not specific to these groups, for they are revealed also in many taxonomic groups of hydroids and in other modular organisms. While this study will not constitute a total and complete analysis of the morphogenetic evolution of hydroid colonies, the main stages are considered – those that define the major directions in morphological evolution within the groups of high taxonomic rank.

Our focus will be on a consideration of macro-morphogenesis, or morphogenesis at the supra-cellular level, rather than on the molecular and biochemical mechanisms that underlie these processes. Morphogenesis surely depends upon gene expression, but little is known how it is achieved. Moreover, the control of morphogenesis cannot be reduced only to genetic regulation. The greater if not decisive role is played by the rules and laws of the theory of complex systems. Therefore, the interaction of elements within the whole and the influence of the environment upon them undoubtedly play a role in the realisation of

morphogenesis. This means that morphogenesis bears no direct relationship to gene expression.

The main parameters considered are differences (interdependence) in growth rates of different rudiments in the colony, growth of certain rudiments in different directions, the localisation of growth and branching zones, shape of the structure, skeleton formation, etc. Using such morphogenetic characters, nearly 100 years ago Kühn (1914) proposed a simple classification of growth types in colonial hydroids, which was further modified by Naumov (1960). Surprisingly, this approach was not developed further and was not applied in full measure. Perhaps it is the difficulty of investigating growth and morphogenesis in colonial hydroids that led to a distrust of speculative models for them. However, the morphogenetic approach is insufficiently developed even with regard to a description of diversity in plant forms, which are more accessible.

In this paper we took into account the series of papers by Berrill (1949a, b, c, 1950), and 'the theory of biological (embryonic) field' by Gurwitsch (1922) and his followers (Belousov & Ostromova, 1969; Belousov et al., 1972; Belousov & Dorfman, 1974), including the only papers of their kind by Belousov (1975, 1991) on the 'parametric system of hydroids'. However, such works are still few in number, so the method of morphogenetic analysis in classification of forms remains poorly developed.

## Materials and methods

The data and theoretical ideas set forth in this work are based on detailed investigation of all aspects of the biology, growth, morphogenesis, and ecology in 10 species of colonial hydroids: athecates *Clava multicornis* (Forskal, 1775), *Cordylophora inkermanica* (Marfenin, 1983), and *Tubularia larynx* (Ellis & Solander, 1786), and thecate *Dynamena pumila* (L., 1758), *Gonothyrea loveni* (Allman, 1859), *Laomedea flexuosa* (Hincks, 1861), *Moerisia maeotica* (Ostroumow, 1896), *Obelia geniculata* (L., 1758), *Obelia longissima* (Pallas, 1766), and *Orthopyxis integra* (McGillivray, 1842). The results were presented in a series of papers (Marfenin & Burykin, 1979; Burykin & Marfenin, 1983; Kosevich & Marfenin, 1984;

Marfenin, 1984a, 1985a, b, 1987, 1999; Marfenin & Kosevich, 1984; Marfenin & Homenko, 1988; Leontovich & Marfenin, 1990) and in two monographs (Marfenin, 1993a, b).

Nine species were studied in less detail: athecates *Sarsia tubulosa* (M. Sars, 1835), *Sarsia producta* (Wright, 1858), *Rhizogeton nudum* (Broch, 1903), and *Bougainvillia* sp. and thecate *Abietinaria abietina* (L., 1758), *Diphasia fallax* (Johnson, 1847), *Hydrallmania falcata* (L., 1758), *Sertularella gigantea* (Mereschkowsky, 1878), and *Sertularia mirabilis* (Verrill, 1873).

The method of colony mapping by Marfenin (1980) was applied to investigations of living material. It enables one to fix all spatial changes in form and size of the colony. Time-lapse filming and video recording were also used extensively. To supplement these techniques, morphometry of colony elements and histological surveys were also done. Ecological studies were performed under laboratory conditions (Malutin & Marfenin, 1988; Marfenin & Malutin, 1994; Orlov & Marfenin, 1995a, b) as well as in the natural environment (Belorustseva & Marfenin, 2002).

## Results

Four processes collectively play decisive roles in providing the evolutionary growth of complexity of hydroid colony patterns. These are (1) formation of a hard skeleton, perisarc, by soft tissues, (2) changes in ratio between duration of the growth phase and transition to differentiation in interdependent zones of growth, (3) differences in growth rates between adjacent zones of growth within the rudiment, the shoot, or the whole colony, and (4) changes in spatial relationship of growth zones.

Figure 1 shows a simplified scheme of the evolution of colony structure in the Hydrozoa. It illustrates the result of the manifestation of the main morphogenetic tendency: from temporary colonies – through stolonial colonies of different types – to several main trends of increasing complexity in the development of branching shoots. One can see that this scheme corresponds to the subdivision of hydroids into its main morphological groups: the athecates, thecate, hydrocorals, siphonophores, etc. For simplicity, representatives of only certain hydroid families are shown, and

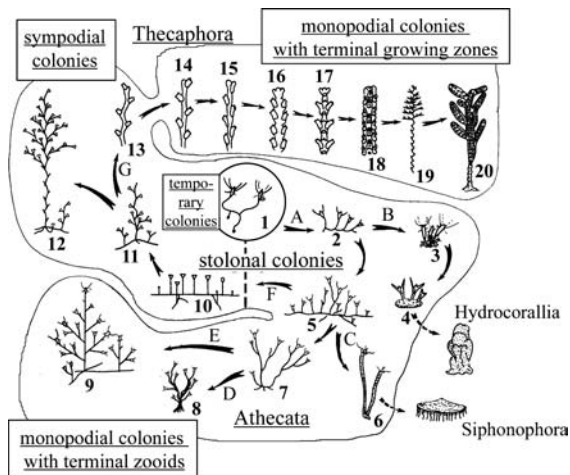


Figure 1. Proposed scheme of morphogenetic evolution of colony pattern in Hydrozoa. Numbers correspond to the species used as examples. *Limnomedusae*: (1) *Moerisia maotica* (Ostroumow, 1896), (2) *Moerisia pallasi* (Derzhavin, 1912). *Athecata* (*Anthomedusae*): (3) *Clava multicornis* (Forsk., 1775), (4) *Hydractinia echinata* (Fleming, 1828), (5) *Cladonema radiatum* (Dujardin, 1843), (6) *Tubularia* sp., (7) *Coryne lovenii* (M. Sars, 1846), (8) *Eudendrium rameum* (Pallas, 1766), (9) *Cordylophora caspia* (Pallas, 1771). *Thecaphora* (*Leptomedusae*): (10) *Orthopyxis integra* (McGillivray, 1842), (11) *Gonothyrea loveni* (Allman, 1859), (12) *Obelia longissima* (Pallas, 1766), (13) *Sertularia pellucida* (Jaderholm, 1908), (14) *Sertularia nana* (Hartlaub, 1901), (15) *Sertularia suensoni* (Levinsen, 1913), (16) *Thuiaria carica* (Levinsen, 1983), (17) *Sertularia staurotheca* (Naumov, 1960), (18) *Thuiaria mereschkowskii* (Kudelin, 1914), (19) *Thuiaria tetrastrata* (Naumov, 1960), (20) *Thuiaria zachsi* (Feniuk, 1947). Main points of changes in colony structure: (A) from temporary to permanent colony; (B) stolonial colonies become more compact, formation of stolonial mat with thickened perisarc; (C) increasing of hydranth size and reduction of stolonial structures; (D) formation of polysiphonous shoots; (E) regularity in branching of shoots; (F) from athecates to thecates; (G) decreased hydranth size, increased branching regularity and general complexity of colonies. Dotted line (between 5 and 10), border between athecates and thecates.

among them Sertulariidae looks mostly indicative, concerning evolution of shoot's construction.

#### Formation and functions of the outer skeleton

If we accept that colonial hydrozoans have originated from solitary ones on the bases of unfinished vegetative reproduction (Spenser, 1898; Ivanov, 1968; Beklemishev, 1969), then perisarc could help keep the zooids connected with one another. First it provided protection for dormant stages of the organism. Later the perisarc came to be used for

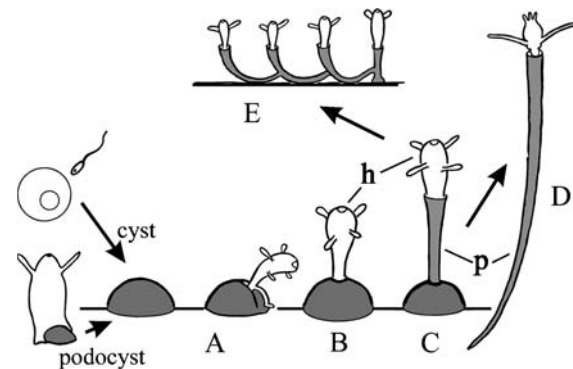


Figure 2. Acquisition of perisarc and alteration of its function. (A) Protection of dormant stages. (B) Attachment to substratum. (C) Protection plus support. (D) Support of elevated structures. (E) Connection of zooids. h Hydranth (zooid); p, pedicel of a hydranth. Perisarc is shaded grey. Podocyst: dormant stage, also used for asexual reproduction in some species of hydrozoans, more common for scyphozoans; a type of cyst formed by the basal part of a solitary polyp (foot) and covered with perisarc.

firm attachment of the organism to its substrate. As the transition occurred from temporary to permanent colonies, it appeared to be effective both in maintaining the inter-zooid connection and in providing support and protection of those structures elevated off the substrate (Fig. 2). But, by its rigidity, it imposes restrictions on the shape and size of the enclosed soft tissues by limiting further growth in certain directions. On the whole, these supportive and protective functions provide the basis for evolutionary development of elevated structures – hydranths with long pedicels or shoots with numerous hydranths.

#### Changes in duration of growth of the rudiment before and after differentiation of a hydranth

The evolutionary development of shoots bearing numerous hydranths went along two main alternative paths (Fig. 3):

- (1) Athecate hydrozoans are characterised by an early development of hydranth structures – tentacles and hypostome – on the rudiment, followed by further growth of this poorly differentiated hydranth for some period of time. In addition, most athecates prolong functioning of the growth zone beneath the terminal hydranth, thereby causing formation and elongation of its pedicel and giving rise to lateral branches.

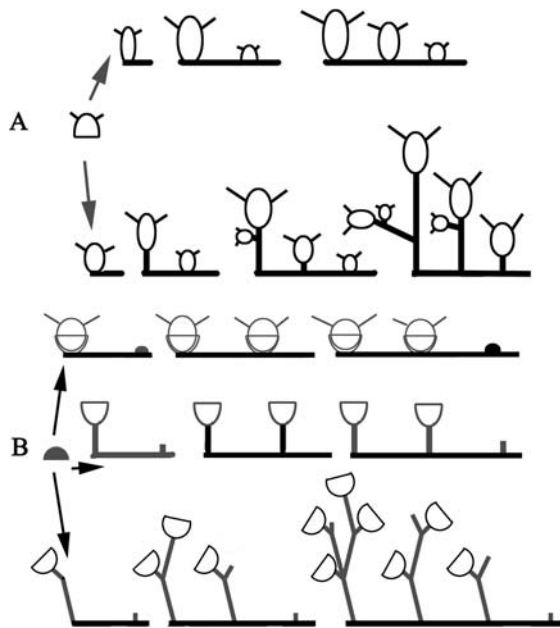


Figure 3. Two strategies in shoot evolution. (A) Long-functioning sub-terminal growth zone (athecaes). Continuous branch elongation and hydranth growth. Top series e.g., *Clava multicornis*, *Rhyzogeton nudum*, *Hydractinia* spp. Bottom series *Cordylophora caspia*, *Bougainvillia* spp., *Pennaria* spp. (B) Temporal terminal growth zone (thecaes). Fixed sizes of the hydranths and internodes. In middle and bottom series only hydrothecae without hydranths are shown. Top series – e.g., *Filellum serpens*, *Cuspidella mertensii*. Middle series – e.g., *Orthopyxis integra*, *Calicella syringa*. Bottom series – e.g., *Obelia* spp., *Campanulina lacerate*. In all cases, distances between hydranths or shoots remain fixed after their formation.

Growth of the main and lateral pedicels continues indefinitely.

- (2) Thecate hydroids display another way. Limited duration of growth zone function produces a full-sized hydranth incapable of further growth. If a pedicel forms beneath it, its elongation is of limited duration, so that if the pedicel is to continue to lengthen, successive emergence of new growth zones is necessary.

#### Arrangement of growth zones within the colony

In the monopodial shoots of athecaes, each branch has one growth zone. Due to the continuous nature of growth in this zone, the distance between hydranths increases through time (Fig. 3A, lower scheme). Such structural organisation from the morphogenetic point of view is a blind alley.

By contrast, in the sympodial shoots of thecaes, the growth zone at the tip of the pedicel functions only temporarily, until a hydranth differentiates at its tip (Fig. 4). Then a new growth zone must appear to continue elongation of the shoot. That is, growth of the shoot is cyclic. In such cases, further evolution of the thecate shoot structure becomes possible due to changes in timing between the completion of hydranth formation (the cessation of activity in one growth zone) and emergence of the next growth zone. The shorter this time interval, the less is the distance between the two adjacent rudiments (Fig. 5A). Figure 5B illustrates the morphological consequences, using several species of the Campanulariidae. Note that when the time interval is short enough, the two growth zones are so close that they fuse. When this occurs, as in some species of *Halecium*, the growing tip divides into two rudiments, one giving rise to a hydranth, the other to the start of the next shoot internode.

From the *Halecium* pattern of sympodial growth, little further change is required to transition to the monopodial form of shoot growth with a terminal growth zone. Indeed, this transition is evident when comparing several genera of the Sertulariidae (Fig. 6). The transitions from I to IV in Figure 6 illustrate an increasing physical association between the hydrotheca and the perisarc of the next internode rudiment, and this is determined by how much the hydrotheca grows after splitting of the tip. If the hydranth rudiment grows for some time after the tip splits, its hydrotheca will be joined to the stem only or largely at its base

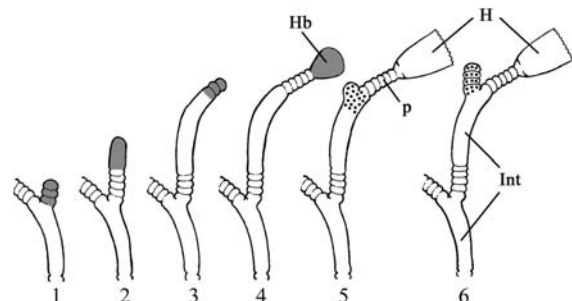


Figure 4. Morphogenetic cycle of the shoot with sympodial mode of growth. 1–6, successive stages. H, hydrotheca; Hb, hydranth bud; Int, shoot internode; p, hydranth pedicel. Consecutive growth zones are shaded grey and dotted respectively.

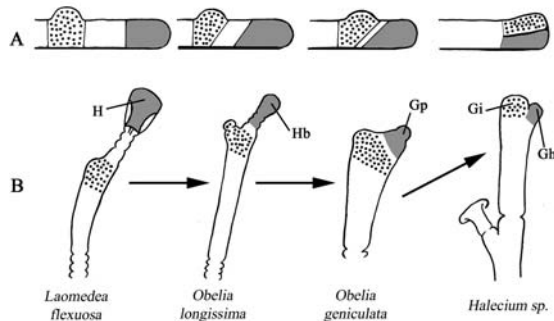


Figure 5. Convergence and fusion of successive growth zones. The terminal growth zone is shaded grey. The next growth zone is dotted. (A) Four steps in the sequence of events, shown schematically, left to right. (B) Examples of each step from three species of Campanulariidae and Haleciidae. Gh, growing zone (rudiment) giving rise to a hydranth; Gi, growing zone (rudiment) giving rise to the next shoot internode; Gp, growing zone started formation of the hydranth pedicel; H, immature hydranth; Hb, hydranth bud.

(Fig. 6 I and II). But if the hydranth completes its growth quickly relative to the rate of tip elongation, its hydrotheca will be fused laterally with the perisarc of the shoot and its orifice will be located at the level of the stem surface (Fig. 6 III and IV). Naumov (1960) was the first who noted the phenomenon of 'hydranth sinking into the hydrophyton,' along with the evolutionary growth of complexity of the shoot structure.

In stolonial colonies, in sympodial shoots, and in monopodial shoots with terminal hydranths, the growing tip represents a radially symmetrical and balanced structure. But the transition toward subdivision of the growth zone into two rudiments opens a new phase in the evolution of shoot morphogenesis and structure. As subdivision of the growing tip into separate hydranth and stem rudiments occurs earlier and earlier prior to differentiation of the hydranth (that is, toward the right side of Figs 5 and 6), the tip becomes asymmetric and unbalanced. The consequences of such a phenomenon are discussed in detail in the works by Belousov (1975, 1991). The asymmetry of the growing tip underlies the origin of diverse morphologies of different species.

Early emergence of the next shoot internode growth rudiment within the growth zone of the underdeveloped previous internode leads to formation of a shoot bearing hydranths arranged in

one, two, or several rows. The number depends upon the number of partitions set up by the growing tip, their mutual spatial arrangement, and their growth rates. On the whole, the morphogenetic cycle of internode formation becomes more complex, including the development not of one but of several hydranths prior to return of the tip's shape back to its starting condition. This can be illustrated by shoot growth in *Abietinaria abietina* (Fig. 7). After separation of the branch and hydranth rudiments in Figure 7A, the growing tip changes significantly in form, becoming less broad. Only after formation of the third hydranth rudiment farther on does the growing tip start to return to its original appearance (compare in Fig. 7, A with G). In this way, the morphogenetic cycle of the shoot internode incorporates the formation of a lateral branch rudiment that leads to regularity of branching (the branches are formed obligatorily in a certain order, at a certain (predictable) position and at certain (and constant) distances from one another).

#### Ratio between growth rates throughout the colony

The shape of the colony depends in large part upon the relative duration and rate of growth of its parts. This can be illustrated most clearly in the shape of its shoots.

If the branches arise regularly and all grow with equal and constant rates, then the shoot becomes spear-shaped, as in young shoots of *Sertularia murabilis* (Fig. 8A). If the growth rate of the branches slows with age, then the shoot appears lancet-like, as in *Diphasia fallax* (Fig. 8B). If the elder branches resorb, the shoot looks like a pine tree with a naked proximal part, as in old shoots of *S. mirabilis* (Fig. 8C). If the branching and growth rates of the branches are irregular, such shoots attain diverse shapes, as in *Gonothyrea loveni* and *Dynamena pumila* (Fig. 8D). In some species all lateral branches give rise to frustules, the result being that even though many branches are formed, the stem appears to be only weakly branched, as in *Obelia geniculata* (Fig. 8E). Finally, many species from different groups show a definite ratio in the duration and growth rate of branches of successive orders, which leads to a species-specific shape of the shoots, as in *O. longissima* and many species of Aglaopheniidae and Plumulariidae (Fig. 8F). The shape of

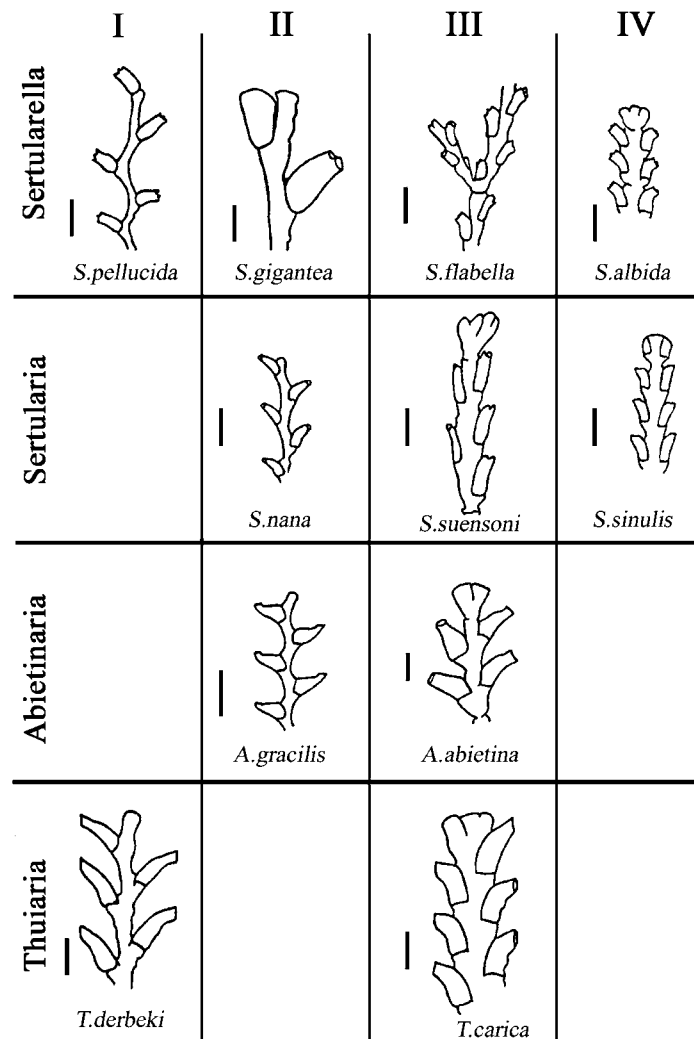


Figure 6. Examples of transition from sympodial mode of shoot growth (I) towards the monopodial with terminal growth zone (IV) within four genera belonging to Sertulariidae. Species names are according to Naumov (1960). Scale bar: top row, 1 mm; the rest, 0.5 mm.

the shoots is achieved due to the differences in the size (length and diameter) of the internodes and duration of growth between the stem and branches of different orders: the higher the branch order, the shorter is the length of the branch. Resorption of the old branches plays a role, too.

### Discussion

The main tendency in the evolution of colonial hydroid morphology is integration of the colony

gradually toward the level of a unitary, non-modular, organism. In the course of such evolution, the colony as a whole gains individuality as the component zooids lose their individuality (Beklemishev, 1969). With regard to the four morphogenetic processes described above that determine colony form in hydroids, one can imagine an evolutionary tendency toward more complex colony structure: from a temporary colony toward a permanent one with highly organised shoots along which hydranths and branches are localised in a strictly arranged manner.

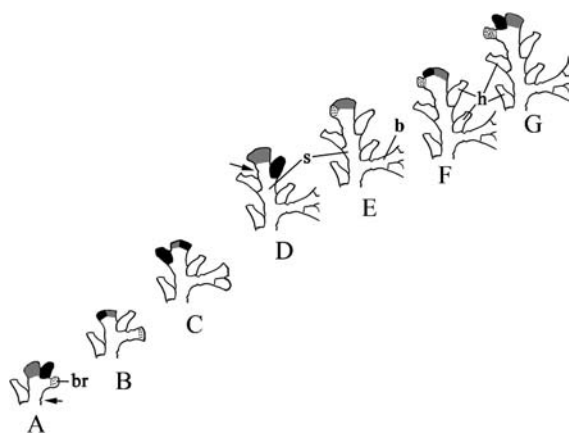


Figure 7. Complex morphogenetic cycle of the shoot internode development in *Abietinaria abietina* (Sertulariidae), including formation of a lateral branch and three hydranths. b, lateral branch; br, branch rudiment; h, hydranth; s, shoot stem. Hydranth rudiment is black, lateral branch rudiment is dotted, stem rudiment is shaded grey. Arrows indicate the furrow on the perisarc surface which is usually believed to be the sign of the borders between the internodes. A–G, successive stages: (A) Beginning of the internode formation; wide growing tip subdivided into tree rudiments. (B) Splitting of the second hydranth rudiment. (C) Splitting of the third hydranth rudiment; end of the internode formation. (D) Beginning of the next internode formation; widening of the growing tip. (E) Splitting of the branch rudiment. (F) Splitting of the first hydranth rudiment. (G) Stage in the stem growth equivalent to A.

A comparative morphological analysis of a large number of Leptolida species, together with an investigation of shoot morphogenesis in certain species, allow us to assert that the main morphological mechanism for achieving structural complexity in hydroid colonies is the early emergence of the next rudiment or growth zone; that is, a convergence followed by fusion of adjacent growth zones. This is a variant on typical heterochrony, which is well known to play an important role in the evolution of many organisms (Gould, 1977; Raff & Kaufmann, 1983; McKinney & McNamara, 1991). The efficiency of this process is increased by the establishment of a shoot morphogenetic cycle during which branching regularity and hydranth development, its duration, size and shape, are determined.

Convergence of the growth zones (that is, shortening of the period prior to emergence of the next growth zone) during the intermediate stage of increasing of morphogenesis complexity opens up possibilities for variability. Even Berrill (1949a) gave

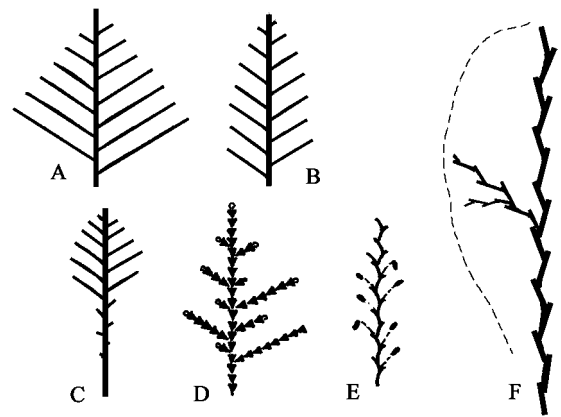


Figure 8. Effect of correlation between growth rates and duration of growth of branches upon the shoot shape in colonial hydroids. (A) Regular branching and constant growth with constant rate. (B) Regular branching and slowing-down of growth rates with age. (C) Like in A or B plus resorption of old branches. (D) Irregular branching and unsteady growth rates. (E) Transformation of lateral branches into frustules. (F) Regular differences in the growth rates and duration of growth between branches of successive orders. For simplicity, only one branch of the first order and one branch of the second order are shown. The contour of the shoot (one side) is outlined by the dotted line; at the base of the stem old branches undergo resorption. In A, B, C, and F, the diameter of the branches is about the same as that of the main stem.

examples of the next terminal hydranth bud emerging at different times in *Obelia geniculata* (Campanulariidae) and *Schizotricha tenella* (Plumulariidae). As a result, growth of the lateral rudiment could even surpass that of the central one that gave rise to it. The evolution of morphogenesis within the Plumulariidae was not studied more, so this example from Berrill adds significant confirmation of the commonness of the patterns under discussion.

One can recognise similar processes in the hydroid group Stylasteridae, in which evolution is affected by calcification of the skeleton (Cairns, 1987). The development of more and more integrated cyclo-systems, or a 'cormidium' in general form (Beklemishev, 1969), takes place due to the convergence of local growth zones. Higher morphological integration of the siphonophoran corium is predetermined by the primordial closing of three growth zones in the larva.

Growth zone integration in the Hexacorallia is achieved in two ways (Marfenin, 1984b). In one, intra-calicle fission takes place earlier and earlier, and as a result the colony is transformed from a

dichotomous one (family Cariophyllidae) to a honeycomb (family Faviidae) and further on into a brain-shape (e.g. genus *Platygyra*). Along the same direction plus predominant lateral branching, increasing structural complexity is realised through the convergence of the growth zones and increasing complexity of the growing tip, as illustrated by the genus *Acropora*.

A decrease in the spatial and temporal interval between the emergence of consecutive rudiments, together with the development of integral (complex, joint) growth zones is a prevailing 'trick' in the evolution of morphogenesis. It can be demonstrated in all modular organisms: different invertebrates, plants, and fungi. These processes can be more easily investigated using colonial hydroids than in other colonial invertebrates, and especially more easily than in unitary organisms.

### Acknowledgments

This research was done at the Moscow State University and supported in part by RFBR Grant #01-04-48798 and another part by Russian Federal Program 'Integracia' Grant #EO265.

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