

Changes in the patterning of a hydroid colony

Igor A. Kosevich

Department of Invertebrate Zoology, Faculty of Biology, M.V. Lomonosov Moscow State University, Vorob'evi Gori, Moscow 119992, Russian Federation

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Abstract

It is a widely held view that colonial hydroids (Cnidaria, Hydroidomedusae) are formed on the basis of a repetition of uniform elements. The dominant opinion is that the equal spatial organisation of the colony exists during all stages of its development except the primary polyp, which develops from the settled larva. However, the complex structure and large dimensions of shoots in certain thecate species (subcl. Leptomedusae) suggest that the organisation of the primary shoot differs strongly from that of established colonies. The present study based on a thorough collection and examination of the collected material allowed to describe the entire sequence of the colony ontogeny in *Hydrallmania falcata* (Sertulariidae). The established shoots of this species are characterised by relatively large size, spiral arrangement of pinnate branches over the shoot stem, and hydranths arranged in one row along the upper side of branches. We showed that the primary shoot developing from the larva has much smaller dimensions and an alternate arrangement of hydranths. During further colony development the shoot organisation undergoes a gradual transformation ending with the emergence of large shoots with 'characteristic' species-specific features. The discovered sequence of changes in shoot patterning shows certain correlations with alterations of the growing tip dimensions. The dimensions of the growing tip seem to determine the patterning in accordance with the particular spatial location of the tip. This finding implies the necessity of a detailed reinvestigation of the entire colony development in thecate hydroids, which would make a significant contribution to the understanding of the morphogenetic evolution and patterning mechanisms within this group of colonial organisms.

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Introduction

Most multicellular animals undergo considerable changes in their body pattern organisation during embryogenesis or post-embryonic development that includes metamorphosis of larvae into the adult organism. During the further life of adult organisms their body pattern remains more or less constant, only the relative size of the body parts can alter. This assertion is

correct for all unitary multicellular organisms. The situation is somewhat different in modular organisms. Body construction on the basis of cyclic morphogenesis provides the basis for a great variability in patterning of common modular parts. The best known examples come from the investigation of plants: the phenomenon of phyllotaxis alteration in certain plants (Malygin 2002), variations in flower organisation (Cubas et al. 1999; Fleming 2005), etc. Less is known about possible changes of patterning in modular animals (the more commonly used term is 'colonial animals'; here the

E-mail address: ikos@hydrozoa.org.

terms ‘modular’ and ‘colonial’ are used as synonyms). It was shown that the pattern of a bryozoan colony can change depending on the contact with substrate (Nikulina 1999, 2000, 2002). Changes in the set of polymorphic zooids in colonial hydroids (Cnidaria, Hydroidomedusae) are another example of possible alteration of patterning during animal ontogenesis.

The hydroid colony can be imagined as a system of branched tubes composed of two tissue layers: outer ectoderm and inner endoderm (gastroderm). Part of the tubes called stolons is attached to the substrate and grows over it. On their upper side stolons bear shoots protruding into the surrounding water in regular intervals. The extremities of the shoots are either occupied with zooids resembling the freshwater polyp *Hydra* or growing tips which are morphogenetic colony elements. Growing tips are morphogenetic elements of the colony and serve to elongate the tubes and shape the new zooids (hydranths) (Fig. 1a). The proliferation takes place in the tissues proximal to the growing tips. From the outside the colony body, except for the hydranths, is covered by a rigid chitinous skeleton called

perisarc. The new perisarc is produced and shaped by the growing tip (Fig. 1b). In athecate hydroids (Hydroidomedusae, Anthomedusae) the hydranths remain ‘naked’, while in thecate hydroids (Boero et al. 1996) the hydranths are surrounded by the tubular or cup-shaped hydrotheca – the zooid housing. Due to the rigid outer skeleton the shape of the colony body is fixed at the moment when the element is formed by the growing tip.

Most colonial hydroids show polymorphism of their zooids. Gastrozooids catch, ingest and digest the food, gonozooids form buds of the sexual stage (medusae) or develop gonophores (reduced medusae) with eggs and sperm, dactylozooids and nematophores have no mouth and serve for defence or prey capture (Braverman and Schrandt 1967; Bouillon et al. 2004). In most hydroids the polymorphic state of the colony is transient and new types of zooids appear after switching to sexual reproduction, or as a response to certain signals from the surroundings (Werner 1958, 1961; Harvell 1994; Widmer 2004). But in certain species and groups of colonial hydroids the zooid polymorphism is a

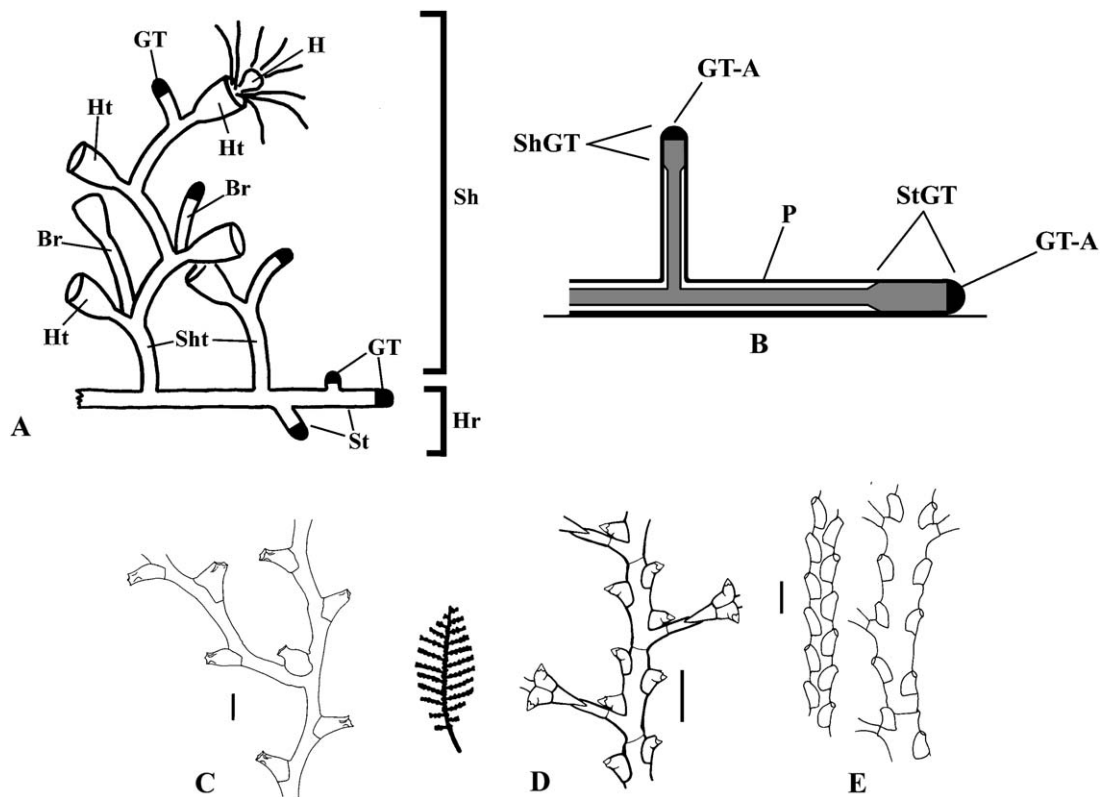


Fig. 1. Structure of the hydroid colony: (a) Schematic drawing of the thecate hydroid colony organisation. (b) Correlation between tissue (shown in grey) and skeleton in a hydroid colony. (c–e) Examples of the colony organisation in the family Sertulariidae. (c) *Sertularella gaudichaudi* (Lamouroux, 1824). Part of a shoot (from Cornelius 1979). Scale bar: 0.5 mm. (d) *Tridentata marginata* (Kirchenpauer, 1864) (from Calder 1990). General shape of the shoot on the left, and part of the shoot on the right. Scale bar: 0.5 mm. (e) *Salacia articulata* (Pallas, 1766). Part of the first-order branch (on the left) and stem (on the right) of a shoot (from Cornelius 1979). Scale bar: 0.5 mm. Abbreviations: Br, branch; GT, growing tip; GT-A, apex of the growing tip (where the new skeleton is exuded); H, hydranth; Ht, hydrotheca; Hr, hydrorhiza; P, outer skeleton (perisarc); Sh, shoots; ShGT, shoot growing tip; Sht, shoot stem; St, stolon; StGT, stolon growing tip.

permanent characteristic feature (e.g. *Thecocardium quadratum*, family Ptilocodiidae [Pfeifer and Berking 1995], families Plumulariidae, Aglaopheniidae [Svoboda and Cornelius 1991; Agis et al. 2001; Bouillon et al. 2004]) like in Siphonophora (Dorit et al. 1991). In such species the spatial arrangement of different zooids can be very strict and is believed to be constant during the colony lifetime and regarded as a characteristic feature especially of thecate hydroids (Hydroidomedusae, Lep-tomedusae).

Sertulariidae show one of the highest levels of integration among thecate hydroids. Their colony is composed only of gastrozooids except for the time of sexual reproduction. The arrangement of the elements within the colony reaches a high level of complexity. The shoots can reach several centimetres in height and bear hydranths in two, three or more rows along the shoot stem and its regular branches (Figs. 1c–e). *Hydrallmania falcata* is a striking example of a complex spatial patterning of the shoot elements (Fig. 2). The shoot

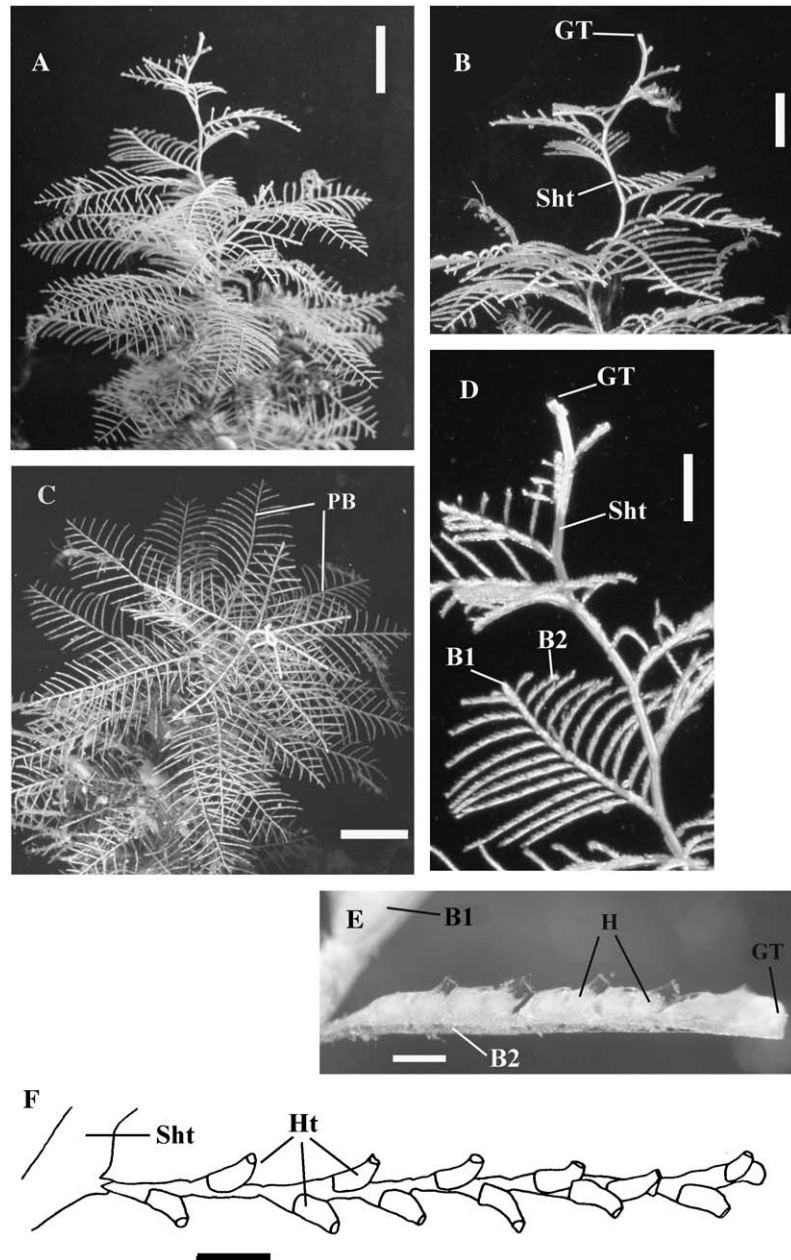


Fig. 2. Structure of 'typical' shoots of *Hydrallmania falcata*. (a, b, d) Lateral view. (c) View from above. (e) Branch of the second order (lateral view). (f) Side-branch with biseriolate alternate hydrothecae (from Cornelius 1979). Scale bars: (a, c) 10 mm; (b, d) 5 mm; (e, f) 500 μ m. Abbreviations: B1, first-order branch; B2, second-order branch; GT, growing tip; Ht, hydrotheca; PB, pinnate branches; Sht, shoot stem.

stem is composed of long internodes, up to several millimetres long that form an open spiral. Each node bears a lateral pinnate branch, and the branches are arranged in a spiral around the stem. The characteristic feature of *H. falcata* is the location of the contiguous hydrothecae on the upper side of the branches in groups of 3–8. The diameter of stem internodes is up to 1 mm, the diameters of the branch axis decrease with their order.

The complex organisation and large dimensions of *H. falcata* provoke the questions how this complexity has developed in the course of evolution and how it develops in the ontogeny of the colony. The hydrozoan colony starts from the primary hydranth that is formed from the settled larva in the course of its metamorphosis. In most known hydrozoan species including *Siphonophora* the larvae have small and relatively equal sizes – their length varies in the range of 75–300 µm, and the diameter is 20–150 µm (Belousov and Ostroumova 1966; Marfenin and Kosevich 1984b; Sommer 1990; Walther et al. 1996; Groger and Schmid 2001) – and serve only for the development of the primary hydranth capable of food uptake. The type and mode of the hydrozoan larvae development and the size of the gonothecae in all species with large shoots (Naumov 1969; Calder 1990; Medel and Vervoort 1995; Agis et al. 2001) allows the assumption that their larvae have similar dimensions. Thus, the material of the larva is insufficient to give rise initially to a stem of large diameter as in *H. falcata*. This means that the primary shoots in the species under discussion obviously have a different pattern of zooid arrangement.

The present paper presents the results of an investigation of shoot development and structure in *H. falcata*. Thorough collection and examination of material allowed the reconstruction of the sequence of colony development from the moment of larva settlement until the appearance of species-characteristic large shoots. The results show the possibility of regular changes in colony patterning during its development and can help to understand how this complexity of the colony patterning has developed in the course of evolution.

Materials and methods

Different substrata – stones, mollusc shells etc. – were collected using SCUBA diving in the vicinity of the M.V. Lomonosov Moscow State University White Sea Biological Station (Kandalaksha Bay, White Sea) at 7–25 m depth. Initially the material was investigated under a dissecting stereomicroscope. Photos were made with the digital camera Olympus Camedia C-4040ZOOM attached to a Wild Makroskop M420.

Animal description

H. falcata (Linnaeus, 1758) (Sertulariidae, Hydroidomedusae, Leptomedusae) is a common hydroid species widely distributed in Atlantic waters around Europe and North America (Naumov 1969) with a very distinctive construction of its shoots. The large shoots can grow for several years. Most works on hydroid systematics only include descriptions of the distinctive large shoots of *H. falcata*. Here, we give such a brief description based on the work of Naumov (1969) and Cornelius (1979).

Colony erect, tall, up to 640 mm; with rootlike hydrorhiza. The main axis is monosiphonic, in a characteristic open spiral of pitch 10–30 mm, with lateral pinnate branches arranged in a spiral around the stem (Fig. 2). Hydrothecae are absent on the stem, they are usually present on one upper side of the branches, but inclined alternately left and right; contiguous, in groups of 3–8, separated by nodal constrictions. Hydrothecae roughly tubular, broadening basally; aperture terminal, circular, even-rimmed. Young colonies and occasionally branches of mature colonies have biseriately alternate hydrothecae (Fig. 2f). Mature colonies with occasional side-branches of this kind appear to occur sporadically within a population, and are not rare.

All those morphological characteristics relate to the outer chitinous skeleton of the colony. The soft tissues are hidden inside it and only the hydranths protrude from time to time from the hydrothecae openings. The outer skeleton of the colony is shaped during growth and does not change later on. It is rather stable and remains intact for a long time even after disintegration of the inner soft tissue, preserving the morphological peculiarities of a living colony. This property of the colony skeleton allows to reconstruct and analyse the sequence of colony development on the basis of samples collected in nature. As most of the specimens were collected within a relatively small sample area (800–1000 m²) one can assume that one homogenous population was studied. So far, full-length studies of *H. falcata* colony development in the laboratory or in the field are not possible.

Scanning electron microscopy

The specimens were fixed in 4% paraformaldehyde, dehydrated in a series of ethanol–water mixtures of increasing ethanol concentration, ending in 100% ethanol, acetone, and critical-point-dried using CO₂ in the Hitachi critical point dryer HCP-1. After mounting upon holders the specimens were sputtered with gold coat in Eiko IB-3 and examined in scanning electron microscopes Hitachi S-405A and CamScan-S2.

Results

The sequence of the early stages of *H. falcata* colony development was reconstructed on the basis of comparative investigation of collected material.

Primary shoots

We found several primary shoots in field material but all of them were dead. They were part of a colony consisting of shoots of different age and size up to those typical of *H. falcata*.

The primary shoots were of minute dimensions and started from a small plate-like base (Figs. 3a and b). The stem of the primary shoot was almost straight and bore two alternating rows of hydrothecae (Figs. 3c–e). At the base of the primary shoot the successive hydrothecae were separated by relatively large parts of free stem. In longer primary shoots the distances between hydrothecae often decreased slightly towards the distal (upper) end of the shoot while the stem diameter remained constant (Figs. 3d and e). No primary shoots with lateral branches were found. In most cases two stolons emerged in opposite directions from the base of the primary shoot. At a short distance from the primary

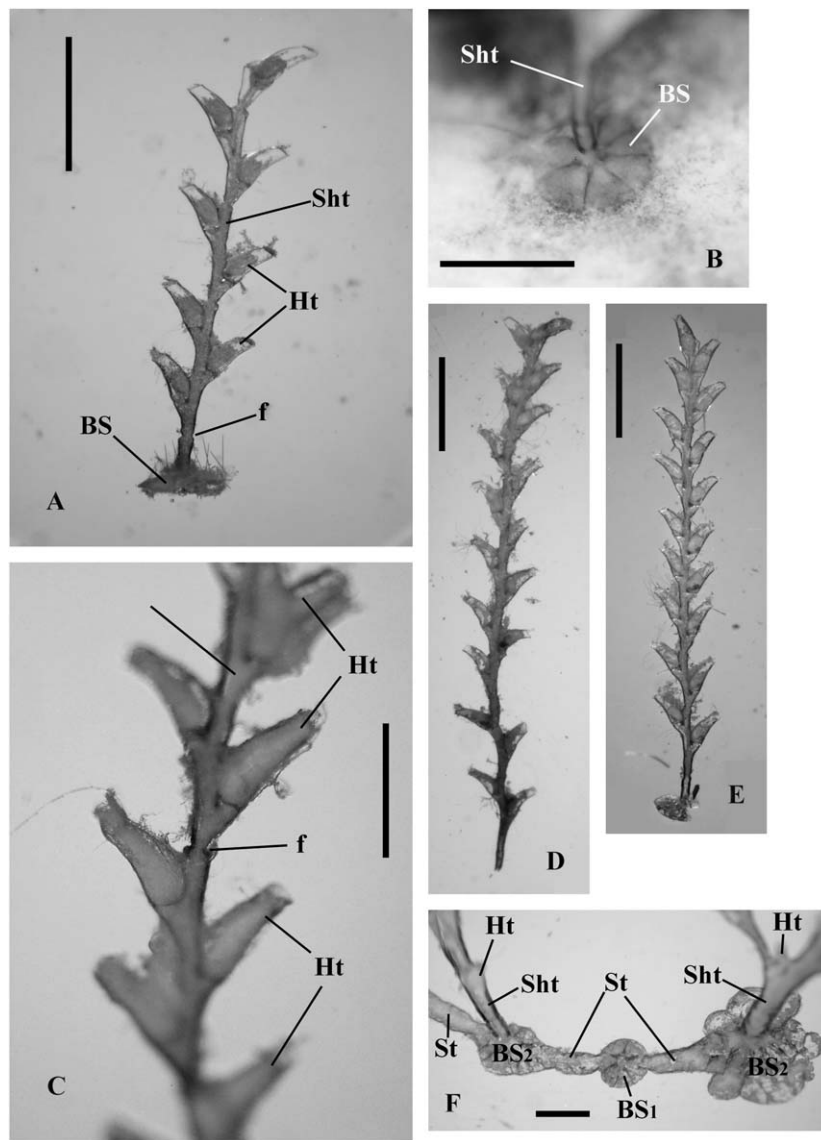


Fig. 3. Details of the primary shoots organisation of *Hydrallmania falcata*. (a) Small primary shoot, lateral view. (b) Plate-like basement of the primary shoot. (c) Detail of the primary shoot. (d, e) Variations of the larger primary shoots, showing a decrease in the distance between adjacent hydrothecae. (f) Base of the young colony with two secondary shoots (the stem of the primary shoot is broken off). *Scale bars:* (a, b, d–f) 1 mm; (c) 500 μ m. *Abbreviations:* BS1, basement of the primary shoot; BS2, basement of the secondary shoot; Ht, hydrotheca; f, furrow of the perisarc; Sht, shoot stem; St, stolon of the hydrorhiza.

shoot the stolons give rise to secondary shoots; thus, a colony starts to form (Fig. 3f).

Secondary shoots

Secondary shoots also originated from a plate-like stolon base but this plate was less circular in shape, and the diameter was larger than that of the primary shoot. The organisation of secondary shoots changed with the distance from the primary shoot and the chronological sequence of their origin in the course of colony development. In general, the earliest 2–4 secondary shoots showed a gradual transition from the patterning of primary shoots towards the ‘typical’ organisation of *H. falcata* shoots (Table 1).

Every new secondary shoot in the row had a larger stem base diameter, until the dimensions of the ‘typical’ shoot were reached (Figs. 3f, 4a, 5e). The overall pattern of the first few secondary shoots did not differ significantly from that of the primary shoot. The stem had two alternating rows of hydrothecae oriented in the plane of the stolon. The first hydrotheca on the shoot stem grew on the side looking towards the primary polyp (opposite the direction of stolon growth) (Figs. 3f, 4a, 5e). The distances between the adjacent hydrothecae on the shoot stem are a function of the diameter: the larger the diameter of the stem, the larger the distance between consecutive hydrothecae (Figs. 4, 5d–f, Table 2). At the same time, the relative length of the stem internode elongates in relation to the internode diameter. Until the diameter and length of the stem internode reach certain values (0.4–0.5 mm for the former and approximately 2.0 mm for the latter), the stem internodes lie in one plane passing through the stem and its stolon. In larger secondary ‘flat’ shoots (with the branches in one plane) the stem was subdivided into clearly demarcated internodes with hydrothecae and branches located in its middle part (Figs. 4e, f). If the length of the stem internode exceeded 2.0 mm, the stem started to shape an open spiral (compare Tables 1 and 2) and successive hydrothecae did not form opposite to each other but rather at the angle of 60–70° as in typical adult shoots.

The main distinction of the small-size secondary shoots from the primary shoot was their branching.

Table 1. Example of alteration of the stem internode dimensions in shoots of *Hydrallmania falcata*

Shoot type (sample size)	Diameter (mm) (mean ± SD)	Length (mm) (mean ± SD)
Primary (99)	0.09 ± 0.01	0.30 ± 0.07
Secondary feather-like (30)	0.45 ± 0.05	1.48 ± 0.45
Secondary spiral (23)	0.50 ± 0.05	2.5 ± 0.51

The branches started at the base of the hydrotheca. In early secondary shoots all branches develop in the plane of the stem so the shoot looks feather-like. The initial branching pattern can be irregular – in most cases branches emerge alternating but with varying intervals. On small-size secondary shoots we often found alternating branches separated by three hydrothecae (Figs. 4b, c, 5d). In large-sized secondary shoots a branch emerged from the base of every hydrotheca formed.

First-order branches

The first branches of small-size secondary shoots had the same pattern of hydrotheca arrangement as the stem: the hydrothecae were arranged alternately in two rows on the upper and lower sides of the branch (Figs. 4b, d). The first hydrotheca formed on the lower side. Such shoots are feather-like, with the plane of symmetry running through the stolon.

Branches developing from thicker stems gradually displayed a different pattern: hydrothecae now grew laterally, inclining alternately left and right (Fig. 5). This displacement was gradual on lower branches and started abruptly in distal branches of small-size secondary shoots and all branches of larger secondary shoots. An interesting point is that within such shoots the hydrothecae of all branches were located on the same side of the stem plane of symmetry that passed through the stolon (Figs. 5d, e).

As the hydrothecae shifted to one side of the branch the distance between adjacent hydrothecae decreased and finally they tightly contacted one another and the branch axis. Moreover, adjacent hydrothecae leaned against each other along the length of their lateral walls. Their bases formed a straight line along the axis of the branch while their distal portions with orifices were curved to the right and left (Fig. 5c). The diameter of the internodes in such branches was slightly bigger than that in the stem of primary shoots and was about 0.11–0.14 mm. In plain secondary shoots branches of the first-order seldom-formed second-order branches.

As soon as the stem of the secondary shoot started its spiral growth the pattern of the first-order branches changed. The diameter of the branch axis became larger (Table 3) and the bases of hydrothecae now formed two close lines while the distal ends of the hydrothecae inclined alternately left and right (Fig. 6e). At the base of the branch these rows of hydrothecae started on the lateral side of the branch, shifting further towards its upper side with increasing distance from the base. The axis of the branch is subdivided into internodes by furrows of perisarc. Each internode includes three hydrothecae and the base of the second-order branch. The second-order branch starts at the base of the

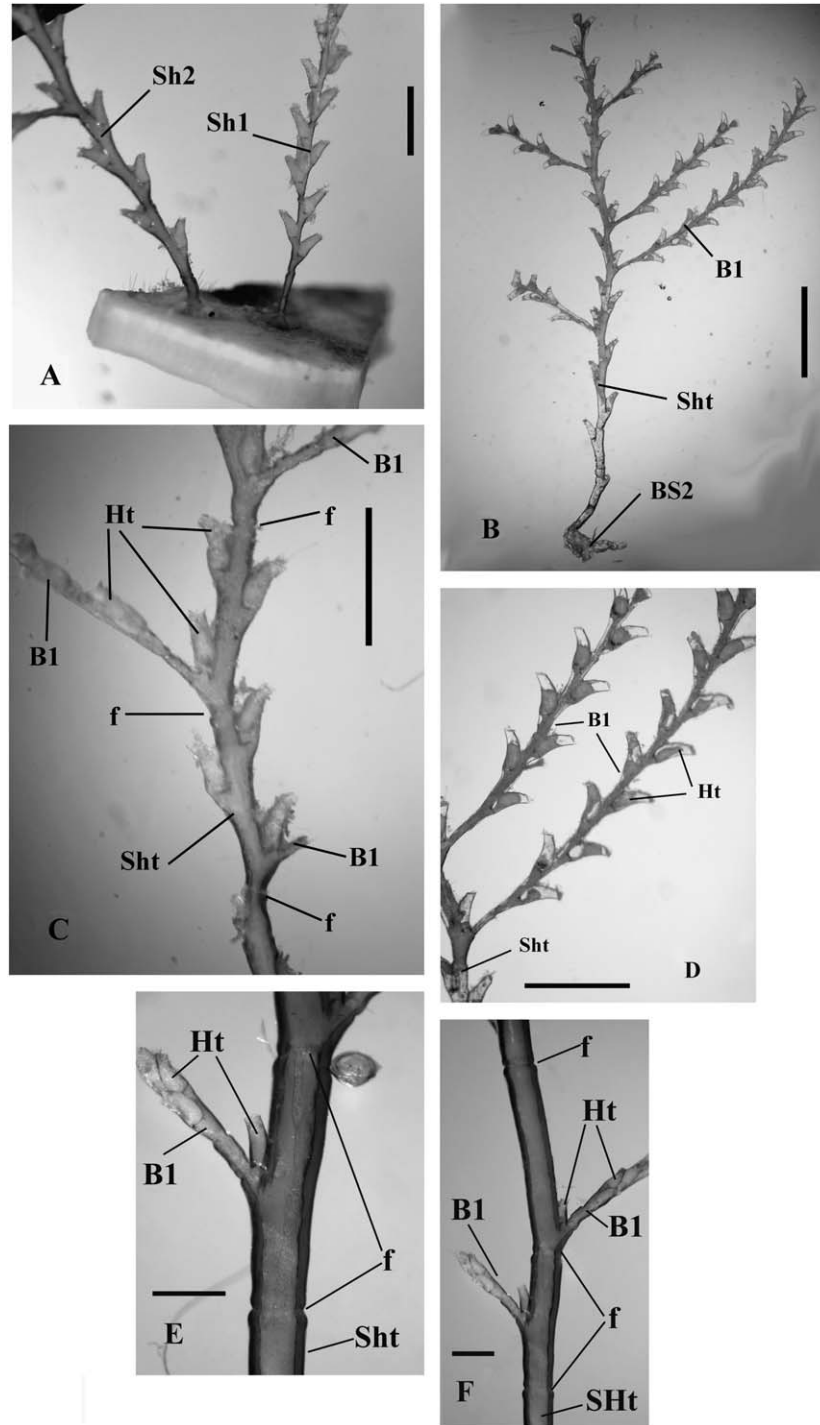


Fig. 4. General organisation of small-size secondary shoots in *Hydrallmania falcate*: (a) Two-shoots colony. (b) General view of a small-size secondary shoot. (c) Portion of the stem of the secondary shoot. (d) First-order branches with alternate hydrothecae arrangement. (e) The stem internode with the base of the first-order branch in the middle part. (f) Shift of the first-order branch base to the proximal part of the stem internode. *Scale bars*: (a, c, d) 1 mm; (b) 2 mm; (e, f) 0.5 mm. *Abbreviations*: B1, first-order branch; BS2, basement of the secondary shoot; Ht, hydrotheca; f, furrow of the perisarc; Sh1, primary shoot; Sh2, secondary shoot; Sht, shoot stem.

first hydrotheca of the internode, on the same lateral side of the axis of the first-order branch to which the hydrotheca inclines (Figs. 6e, g). Deviations from this

pattern are very rare. Therefore the branch of the first order looks pinnate, with regularly alternating second-order branches.

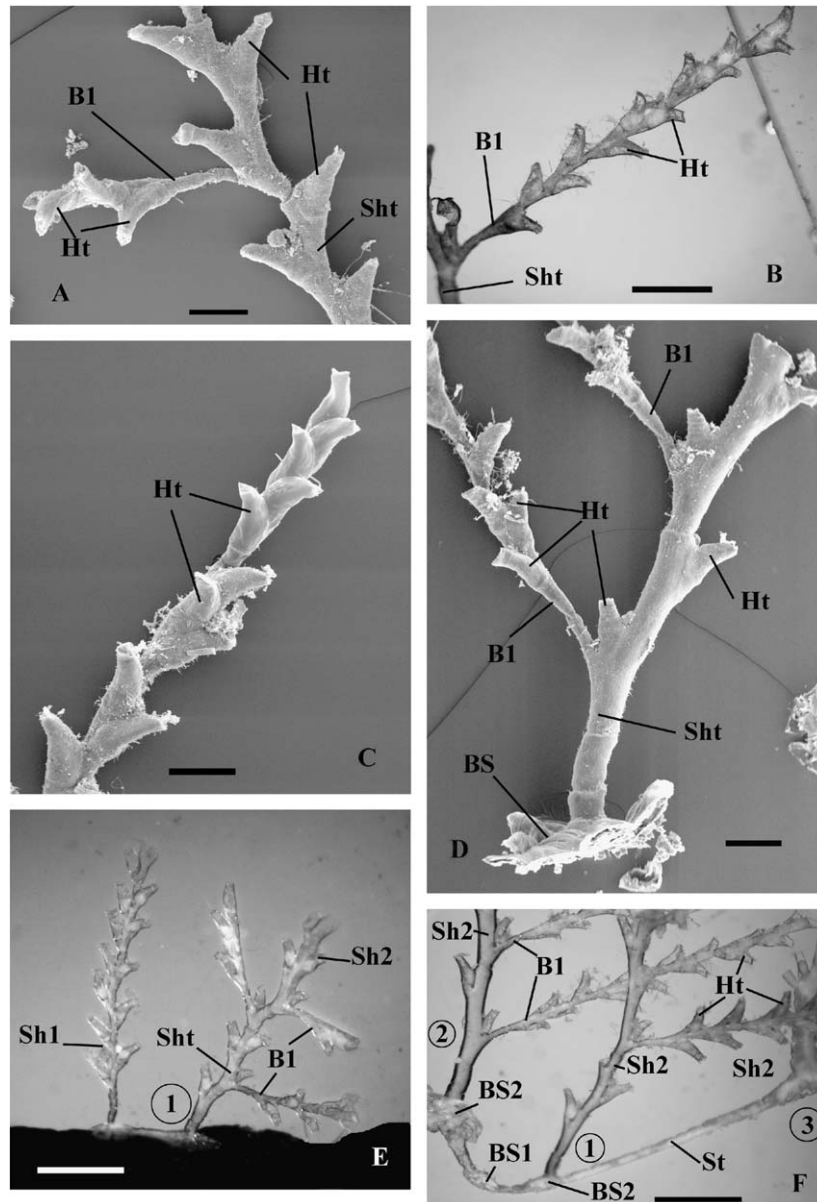


Fig. 5. Gradual transition from biseriata alternate hydrotheca arrangement towards one row of hydrothecae on the upper side of the branches in *Hydralmania falcata*. (a–d) Variations of the transition in hydrotheca arrangement within small-size secondary shoot branches of the first order. (e–f) Variations in organisation of the shoots in young colonies. Numbers in circles indicate the order of the secondary shoot appearance. *Scale bars:* (a, c, d) 300 μ m; (b) 500 μ m; (e, f) 1 mm. *Abbreviations:* B1, first-order branch; BS1, basement of the primary shoot; BS2, basement of the secondary shoot; Ht, hydrotheca; Sh1, primary shoot; Sh2, secondary shoot; Sht, shoot stem.

Second-order branches

The bases of the hydrothecae on the upper side of the second-order branch formed one straight line while their distal ends inclined alternatively left and right. Furrows of the perisarc subdivided the axis of the second-order branch into internodes of varying length: each internode included mostly 3–5 hydrothecae, with variations in the range of 2–9. Irrespective of the furrow position the order of the hydrotheca inclination did not alter – every hydrotheca inclined to the opposite side with respect to

the preceding one. The long axis of the second-order branch formed an angle of about 60–70° with the axis of the first-order branch. All second-order branches lay in the same plane perpendicular to the stem axis.

Adult shoots

The base of the large ‘typical’ shoot was not ‘rootlike’ but showed a widening of the hydrorhiza or stolon, which is not exactly symmetrical. The upper surface as

Table 2. Examples of changes of the stem internode dimensions in feather-like and spiral parts of the same secondary shoots of *Hydrallmania falcata*

Shoots (sample size)	Internode length (mm) (mean ± SD)	Internode diameter (mm) (mean ± SD)	L/D^a	Cor (L/D) ^b
1-FI (17)	1.22 ± 0.203	0.42 ± 0.016	2.89	0.11
1-Sp (6)	1.98 ± 0.27	0.46 ± 0.04	3.69	0.86
2-FI (4)	1.93 ± 0.73	0.53 ± 0.03	3.62	0.95
2-Sp (3)	2.92 ± 0.29	0.51 ± 0.01	5.73	0.99
3-FI (7)	1.70 ± 0.33	0.44 ± 0.03	3.84	0.39
3-Sp (10)	2.77 ± 0.44	0.52 ± 0.05	5.33	0.57

FI – feather-like basal part of the shoot, Sp – spiral distal part of the shoot.

^aRatio between internode length L and diameter D .

^bCorrelation between internode length L and diameter D .

well as the internal partitions of this widening base displayed numerous folds (Figs. 3f and 6a). The stem of the shoot was composed of internodes of different length while their diameter was practically constant. The stem internodes did not form a straight line but an open spiral: every internode deviated from the direction of growth of the previous one by an angle of about 30 degrees in a vertical direction and about 60° in the horizontal plane. By definition, each internode ends with a circular furrow, which in *H. falcata* is slightly oblique. Just above the furrow and close to its lower side a branch originates. Thus, in adult spiral shoots the first-order branch emerges at the proximal end of the stem internode. In contrast to descriptions by Cornelius (1979) a hydrotheca was found at the stem in the sinus of all branches (Figs. 6b, c).

The first-order branches displayed a row of hydrothecae on their upper side but the initial hydrothecae of all first-order branches grew in a lateral position (see above) (Fig. 6e). As the branch of the first order grows, the diameter and length of its internodes slightly decrease and the elongation of the branch slows down (Fig. 7). First-order branches are pinnate: alternate second-order branches emerge in regular intervals at the proximal part of the internodes of the first-order branch (Figs. 6e, g). The branches of the second order are relatively short, they do not branch, and they are also subdivided into internodes by furrows in the perisarc (Figs. 2e, 6e, f). The diameter of the axis of the second-order branch decreases slightly towards its distal end. After formation of 3–5 internodes (about 15–20 hydrothecae) the branches of second order cease their growth.

Therefore the contour of the first-order branch is lancet-like.

The main steps of the changes in spatial organisation of shoot modules during *H. falcata* colony development can be summarised as shown in Fig. 8. The stage in colony development at which adult spiral shoots appear depends most likely upon the amount of nutrition obtained by the young colony. In all primary shoots the size of the hydrothecae and stem are equal, but they differ in the number of hydrothecae. The higher the primary shoot the quicker is the whole process of transformation from ‘primary’ shoot organisation into the ‘typical’ organisation.

It is worth mentioning that the dimensions of a hydrotheca do not change in the course of colony growth (Table 4), but in the primary shoot (1) the hydrothecae are not inclined alternately left and right as can be observed in large adult (‘typical’) shoots, and (2) the hydrotheca walls are less fused with the stem (compare Figs. 3c and 6f, g).

Discussion

Modular organisation provides certain ecological advantages as compared to the unitary organisation of multicellular organisms (Marfenin 1993). In most cases the body of modular organisms has an unlimited mode of growth and the general contour of the ‘colony’ depends upon the environment. The construction of the whole body by the repetition of an unlimited number of

Table 3. Comparison of the average internode dimensions in different parts of the large spiral shoot of *Hydrallmania falcata*

Part of the shoot (sample size)	Internode diameter (mm) (mean ± SD)	Internode length (mm) (mean ± SD)	Correlation between length and diameter
Stem (9)	0.61 ± 0.03	2.97 ± 0.58	–0.24
First-order branch (42)	0.33 ± 0.05	0.93 ± 0.10	0.63
Second-order branch (24)	0.17 ± 0.02	0.84 ± 0.14	0.45

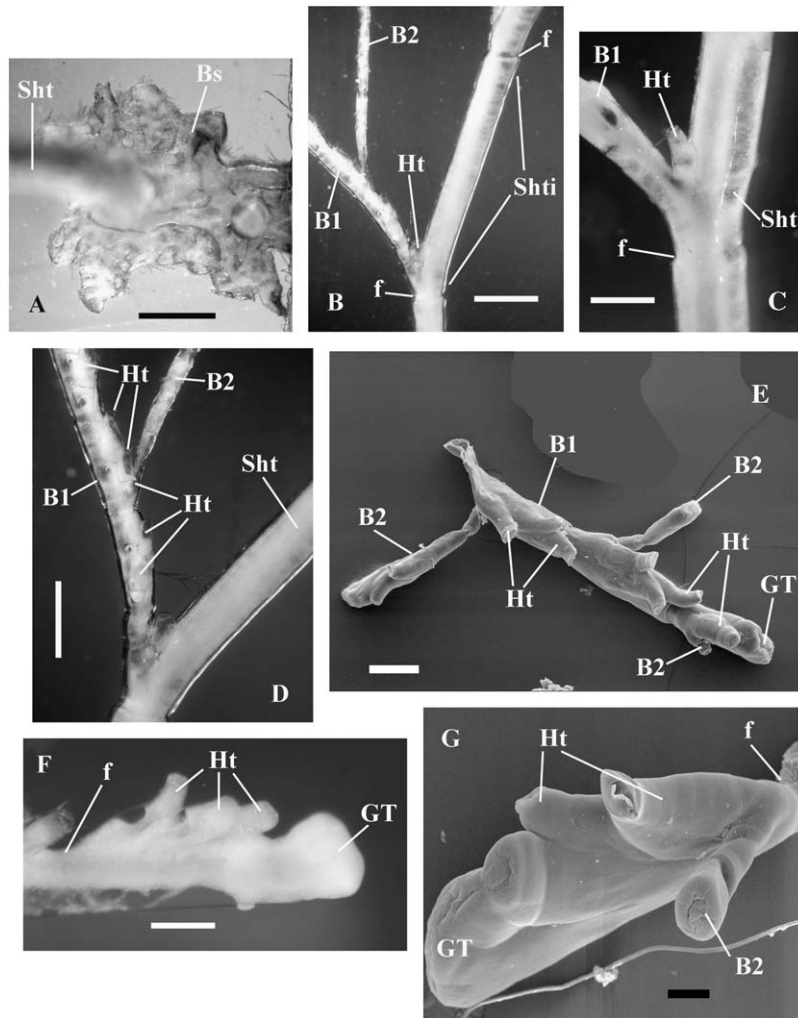


Fig. 6. Details of the large shoot structure in *Hydrallmania falcata*. (a) Basement of the shoot stem – widening of the hydrorhiza. (b) Shoot stem internode. (c) Stem node. (d) Proximal part of the first-order branch, showing displacement of hydrothecae. (e) SAM image of the branch organisation. (f) Side view of the second-order branch-growing end. (g) SAM view of the first-order branch internode. Scale bars: (a, b, d) 1 mm; (c, f) 500 μ m; (e) 300 μ m; (g) 100 μ m. Abbreviations: B1, first-order branch; B2, second-order branch; BS, shoot basement; f, furrow of the perisarc; GT, growing tip; Ht, hydrotheca; Sht, shoot stem; Shti, shoot stem internode.

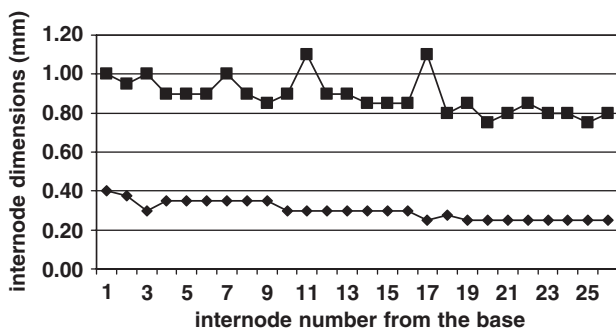


Fig. 7. Example of changes in length (—■—) and diameter (—●—) in a first-order branch internode in a spiral shoot of *Hydrallmania falcata*.

several modules increases the ecological plasticity of such organisms and allows a high level of adaptation to ecological refuges especially in varying environments (Buss 1979; Hughes and Jackson 1990; Marfenin 1997; Sanchez and Lasker 2003).

The ecological advantages of a modular organisation have long been recognised. And for a long time colonial animals were discussed as having no distinct patterning of the entire body. Only a few decades ago it was shown that colonial hydroids possess an organism level of integration which is expressed in constant quantitative proportions and interdependence of the number of colony elements (modules) (e.g. Marfenin 1977, 1997; Marfenin and Kosevich 1984a; Marfenin et al. 1999). At

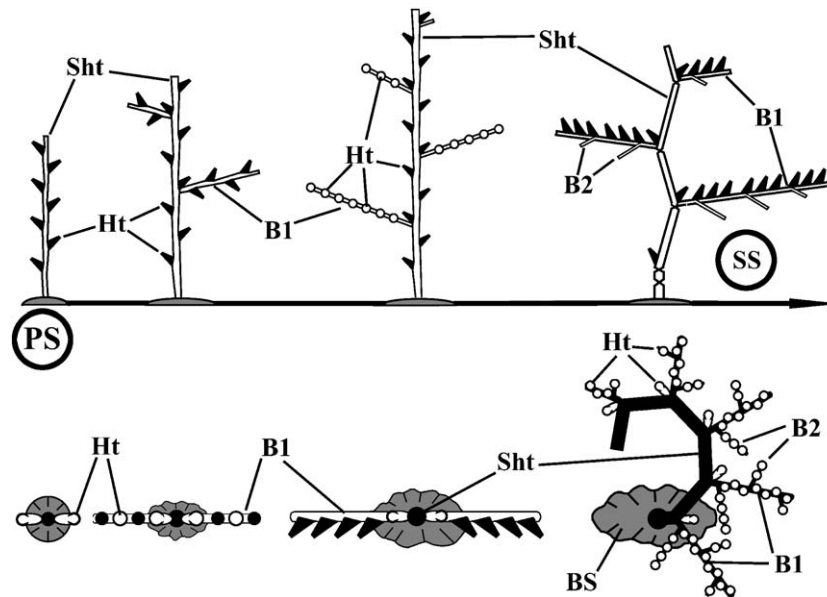


Fig. 8. Schematic drawing of the main changes in spatial arrangement of the elements during the development of a *Hydrallmania falcata* colony from the primary (PS) to the ‘typical’ secondary spiral shoot (SS). Upper row: lateral view in a plane passing through the stolon, lower row: view from above. *Abbreviations:* B1, first-order branch; B2, second-order branch; BS, shoot basement; Ht, hydrotheca; Sht, shoot stem. Black triangles – lateral view of hydrothecae (the longitudinal axis of the hydrothecae lies in the image plane); open circles – view from the direction of hydrotheca opening (aperture); black circle – view from the hydrotheca basement (in the two latter cases the longitudinal axis of the hydrothecae lies perpendicular to the image plane).

first, this was illustrated in thecate colonial hydroids (Leptomedusae) with a relatively high level of colony integration and consistency of morphological features of colony elements. But later on the existence of colony patterning was confirmed for less morphologically integrated athecate colonial hydroids (Athezata, Anthomedusae as well (Leontovich 1991; Pfeifer and Berking 1995).

One of the most obvious manifestations of strict spatial patterning in colonial thecate hydroids is the organisation of shoots in species belonging to the families Plumulariidae, Aglaopheniidae, etc. The high level of spatial patterning of their shoot elements has been well known from taxonomic studies for a long time (e.g. Svoboda and Cornelius 1991; Migotto 1996;

Agis et al. 2001), but the patterning of such complex shoots was rarely discussed (e.g. von Schenck 1965). Each internode includes in a strictly spatially organised fashion a certain number of polymorphic zooids, and this combination serves as a specific character used for species identification. But most taxonomic studies are based on incomplete samples collected by drags. Only recently accurate sampling using SCUBA diving became widely used. Nevertheless, the descriptions of colonial hydroid species remain based on the morphology of the most ‘canonical’ parts of the colony (mostly shoots named ‘colony’). And the dominant paradigm does not change: during colony growth its patterning remains constant in all parts of the colony. Indeed, the normal developmental processes of thecate hydroids are only now becoming understood, and the biggest current problem in hydroid taxonomy is to determine which of the variations between colonies are genotypic and which are phenotypic (Cornelius 1979).

From 1975 onwards, Marfenin and colleagues started a systematic investigation of the deviations of form and element patterning in colonial hydroids (Marfenin 1975, 1988; Marfenin et al. 1995). It became clear that these deviations are not caused by mutations but are manifestations of the faulty operation of the morphogenetic and patterning programmes in the course of element formation. At first such deviations were called ‘anomalies’, but later on the terms ‘malformations’ or ‘morphotypes’ were proposed for some of these deviations. These studies revealed the possibility of changes in

Table 4. Average dimensions of the hydrothecae of primary shoots and from different parts of spiral shoots of a *Hydrallmania falcata* colony

Hydrotheca location (sample size)	Hydrotheca length (mm) (mean \pm SD)	Hydrotheca diameter (mm) (mean \pm SD)
Primary shoot (124)	0.36 \pm 0.03	0.16 \pm 0.01
Stem of the spiral shoot (20)	0.38 \pm 0.03	0.22 \pm 0.02
First-order branch – spiral shoot (25)	0.34 \pm 0.04	0.21 \pm 0.02
Second-order branch – spiral shoot (25)	0.37 \pm 0.02	0.21 \pm 0.01

colony patterning. But the idea was that such ‘malformations’ are temporary and transient phenomena caused in certain cases by strong external perturbations of the environment and, since after the appearance of most such deviations the colony patterning returns to the ‘canonical’ one, they have no causal relationship to possibly regular changes in colony patterning. Even the description of differences in shoot arrangement in *H. falcata* or *Amphisbetia operculata* (Stechow 1925; Cornelius 1979) and a few other species (e.g. *Dynamena quadridentata*, cf. Calder 1990; Migotto 1996) passed unnoticed because of negligible interest in colonial thecate hydroids as a model for developmental biology.

The present study is the first one to show the regular changes in the thecate hydroid colony patterning in the course of its development from a settled planula. So far we have no data on any hydroid colony development that shows comparable events in patterning. In all described cases the development of the colony starts with the formation of the primary hydranth or shoot followed by the appearance of hydrorhiza stolons that give birth to the next hydranths (shoots) in equal intervals. And all shoots have the same pattern of internodes and hydranth arrangement (e.g. *Dynamena pumila*, cf. Marfenin 1977; *Gonothyraea (Obelia) loveni*, *Obelia longissima*, *O. geniculata*, cf. Marfenin and Kosevich 1984a; Kosevich and Marfenin 1986; Marfenin and Khomenko 1988; *Campanularia platycarpa*, cf. Burykin and Marfenin 1983; *Hydractinia echinata*, cf. Blackstone and Buss 1991). The exact contour of the colony and its shoots can differ according to the environmental conditions, but the general pattern of colony and shoot organisation remains constant. The taxonomic descriptions of many thecate hydroid species include mostly the morphological peculiarities of certain stages in colony development.

The colony development in *H. falcata* demonstrates not only the plasticity of the organisation of modular organisms but gives an example of consistent and ordered patterning changes during the postembryonic development of a modular organism. Based on this detailed study of the material on *H. falcata* colony development we present several hypotheses of general importance for hydroid colony patterning and evolution.

(I) The formation of large complex shoots in hydroid colonies with stems of about 0.3–1 mm diameter or more (e.g. *Sertularia mirabilis*, *Thuiaria (Salacia)* sp. (Sertulariidae), *Nemertesia* sp. (Plumulariidae), *Aglaophenia* sp. (Aglaopheniidae), etc.) does not require an enlargement of the larva. The larvae remain of the common size for most colonial hydroids. But the development of the colony will include a gradual transformation of the primary, simply organised shoot into a large and complex one. One of the primary prerequisites for such a transformation is the ability of the colony to increase

and regulate the dimensions of its growing tip, which affects the patterning of the modules. And this ability is not inherent in all hydroids, since in the majority of the thecate species the diameter of the growing tip is more or less fixed.

(II) The gradual acquisition of the ‘typical’ pattern by large shoots of *H. falcata* demonstrates the possible levels of complexity of shoot internode structure and organisation. The first level is the internode of the primary shoot which is composed of a short portion of stem with hydrotheca, as is common in the majority of species with sympodial shoots (Kosevich 1990). The second level is achieved in the secondary small-size shoots with larger stem diameter (Tables 1 and 2) when their branching stabilises and becomes regular. In such cases the development of the stem internode combines several elementary morphogenetic steps into one step. Secondary complex internodes include a regular separation of the lateral branch tip and formation of three primary internodes with hydranths. The border between adjacent stem internodes of the second level is demarcated by the skeleton furrow below the base of the lateral branch (Figs. 3c, 4c, 9a).

The internodes of ‘typical’ large stems demonstrate the third level of complexity of patterning. They are increased in all dimensions (Table 3) but visually include fewer components. At the proximal end each internode is separated from the previous one by an oblique furrow of the skeleton and bears the base of the side

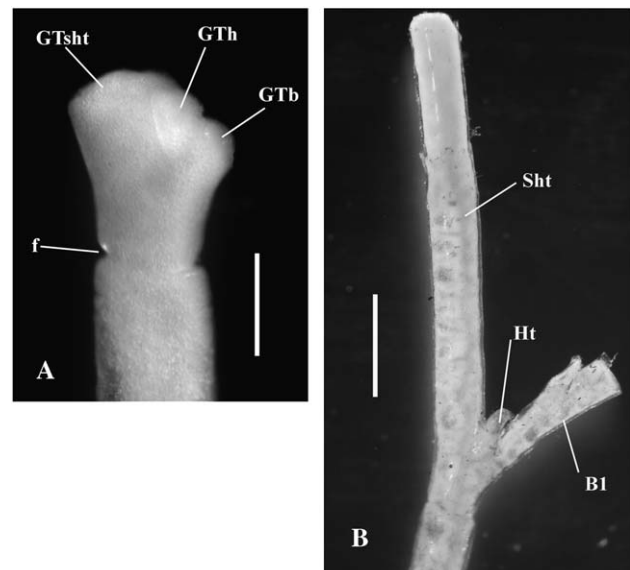


Fig. 9. Some details of the large shoot stem growth in *Hydrallmania falcata*. (a) ‘Compound’ growing tip of the shoot stem. (b) Distalmost internode of the shoot stem. Scale bars: (a) 500 μ m; (b) 1 mm. Abbreviations: B1, first-order branch; Ht, hydrotheca; f, furrow of the perisarc; parts of the ‘compound’ growing tip: GTb, growing tip of a branch; GTh, hydranth rudiment; GTsht, growing tip of the shoot stem.

branch. One hydrotheca is placed in the sinus between the branch base and the stem axis of the internode. It is badly visible and in most cases has no living hydranth. Perhaps that is why in most descriptions of *H. falcata* the stem lacks hydrothecae. Distally follows the smooth cylindrical part of the internode of varying length, free from any additional morphological characters (Figs. 6b, 9b). So in comparison with the internode of the previous level of organisation this one possesses a reduced number of integrated compounds but of increased dimensions. The origin of these internodes is not clear – it could be a real reduction of seriated components (hydrothecae) or an enlargement of the ‘primary’ internode with integration of lateral branch anlagen formation. But it is obvious that the appearance of internodes with this patterning is connected to the increase of the growing tip diameter.

The changes in the patterning of internodes of the first and second order lateral branches are not so prominent. The main differences are (1) the larger diameter of the first-order branch axis and (2) the absence of branch formation in second-order branches. In all other respects the organisation of the branch internodes is more or less similar: they integrate 3–5, seldom up to 7 hydrothecae into one morphogenetic cycle. In that case, too, adjacent internodes are separated by a furrow on the skeleton. All hydrothecae of the internode develop practically simultaneously: the anlagen are separated from the growing tip successively and complete their formation within short intervals (Figs. 6f, g). The hydrothecae anlagen within such an internode are packed closely together, partly overlying one another. And this can cause bending of the hydrothecae orifices in opposite directions.

It is obvious that the patterning of the shoot stem and branches correlates mainly with the diameter of the growing tip. In the case of the smallest diameter of the tip (0.08–0.19 mm) the unbranched shoot structure is formed (primary shoot or second-order branch). An increase of the tip diameter leads to different alterations of the patterning, depending on the shoot part where it takes place. Within the stem, a larger diameter of the tip (up to 0.45 mm) causes a greater length of the internode (segment between adjacent hydrothecae) and regular emergence of the side branch rudiment. Growth of the tip diameter in the first-order branch (up to about 0.20 mm) initiates a displacement of the hydrothecae from opposite sides of the branch toward one lateral side. Further enlargement of the tip diameter gives rise to the following changes in the patterning of the shoot parts: if the diameter of the tip exceeds 0.45–0.50 mm, the stem turns to spiral growth with typical organisation of its internodes: a single hydrotheca in the sinus of the first-order branch base is located at the proximal end of the smooth long internode. Increasing of the first-order branch tip up to 0.40 mm leads to a twist of the branch

axis so that the hydrotheca row is now located on the upper side of the branch, and regular emergence of the second-order branch rudiment.

The most interesting point is that within different parts of the shoot the enlargement of the tip diameter causes different changes in the spatial organisation of the elements. For example, we never observed a stem with increasing diameter passing through the primary shoot organisation, then showing the patterning of the first-order branch with one row of hydrothecae, and then shifting to the spiral organisation. In all cases the shoot parts show a certain spatial-specific order of the pattern changes. At the same time, a decreasing of the tip diameter causes the reverse changes of patterning which cannot be gradual and spatial-specific: a first-order branch of the spiral shoot switches to the growth characteristics of the primary shoot; a spiral stem can show the patterning of the first-order branch of the ‘typical’ shoot and then returns again to spiral growth with increasing of the tip diameter (personal unpublished observations). Such atypical examples of shoot development were helpful in the analysis of patterning mechanisms, but at the moment unfortunately are too few in number. The essential point is that the diameter of the growing tip is not the only patterning mechanism, but works in cooperation with other mechanisms determining the spatial heterogeneity of the shoot.

(III) An interesting question is the role of the furrow in the perisarc of stem and branches. Appearance of the furrow is evidence of an alteration in perisarc hardening: either the tip slows down its growth or the border between the soft and the already hardened perisarc is displaced distally (Kossevitch et al. 2001). In studies on hydroid taxonomy the furrows in the perisarc are regarded as borders of the internodes. If the furrow really demarcates the beginning and the end of the patterning (morphogenetic) cycle then the altering in perisarc hardening has something to do with a change-over from one programme to the next one. And often there is evidence that supports this assumption. The furrows in the *H. falcata* perisarc demonstrate an exact correlation with the borders of morphological units (internodes) of adult shoots. In sympodial shoots of ‘*Obelia*-like’ species (family Campanulariidae: *O. longissima*, *Laomedea flexuosa*, *Gonothyraea loveni*) the furrows in the perisarc correspond to the different steps of internode and hydranth formation (Wytenbach 1968; Kosevich 1990). On the other hand, in certain species of sertulariid hydroids (e.g., *Dynamena pumila*, *D. quadridentata*, *D. crisioides* (Migotto 1996)) the furrows in the shoot perisarc do not always coincide with the borders of morphologically recurring units and are not regular. This can mean that furrow formation is only one of the possible evidences of the borders between consecutive morphogenetic blocks (internode

formation). But in reality the furrow is not obligatory formed and so its presence has low taxonomic value.

(IV) Different types of internode composition in different parts of the shoots raise the question about the role of obviously different patterning mechanisms within the same modular organism. And this patterning does not differ in the variation of integrated or formed components, but in the variation of the spatial arrangement of similar components. These differences strongly support the hypothesis of a high level of organism integration in certain colonial hydroids. In the case in question the patterning of the shoot stem and its branches composed of similar modules (elements) differs so strongly that these shoot parts could be compared to the organs of a unitary organism.

(V) An interesting addition to the discussion of patterning within the shoots of *H. falcata* is the fact that the hydrotheca size remains the most constant character of the internode. Irrespective of the location within the shoot and the age of the shoot all hydrothecae are of the same size. The evolutionary tendency within the thecate hydroids seems to be a stabilisation of the hydrotheca size and a parallel reduction in size to increase the integration and complexity of the colony organisation.

The development of a (modular) organism can be based on several patterning programmes. There seems to be no dominant 'canonical' programme while most others serve as reserved within the epigenetic field of development (Waddington 1962) to withstand external perturbation. On the contrary, the developmental programme can contain several equal variants of patterning and undergo a changeover from one to another depending on external and internal signals. This is a striking example of the complex hierarchical organisation of modular organisms distinguishing them from unitary ones (Rosen 1979; McKinney and Jackson 1989; Sanchez and Lasker 2003).

In conclusion, we can add that the detailed study of colony development in hydroids with highly integrated and complex shoots can help to understand the possible mechanisms and sequences of the evolution of hydroid colony organisation. Such examples support the theory of phylembryogenesis (Severtzov 1945), and allow searching for the exact mechanisms of patterning in different organisms.

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