# 10

# THE FORMATION OF CNIDOCYTE PATTERNS IN SIPHONOPHORES

R. J. SKAER

Peterhouse
Cambridge
England

## SUMMARY

Groupings of cnidoblasts form simple, precise patterns in many cnidarians but particularly in siphonophores. The advantages of using cnidoblasts for the study of pattern formation are described. The information gained allows one to eliminate certain models of pattern formation and to concentrate on behavioral maneuvers of cnidoblasts that sort these cells, align them and merge simpler patterns to make more complex ones. Thus the fundamental constructional units are the clump, the row, and the ability to sort or merge rows. Parameters that are important in the rapid and accurate construction of patterns are discussed in the light of the behavior of migrating cells and of cells undergoing 'contact reassortment.'

## INTRODUCTION

One way by which we hope to learn how tissues are built up is by studying pattern formation. Patterns, particularly if they are simple yet precise, allow certain predictions to be made about where particular cells originate, where they go, how, and possibly why. Cnidoblasts are particularly useful in the study of certain types of pattern formation for they often form very striking yet simple arrays. In siphonophores the arrays are often geometrically exact, are usually made up of fixed numbers of cells, and are set up quite late in differentiation by which time the nematocyst is clearly visible and its type recognizable. The nematocyst thus acts as a label in the cell and in siphonophores one can distinguish at least 7 different categories of cnidoblasts based on nematocyst type, size, etc. Moreover, the nematocyst, by its orientation, can tell us whether the cnidoblast is migrating and the direction of migration (Günzl, 1971; Skaer, 1973). In migrating cnidoblasts the capsule trails behind and the operculum is oriented towards the rear of the cell. At the end of migration, however, the capsule rotates through 90° so it lies apically in the cell and orients with its axis normal to the surface (Wood & Novak, 1982; Novak & Wood, 1983). Thus one can distinguish between cells that are migrating and cells that are positioning themselves after migrating. Moreover, the orientation of the nematocyst about its long axis, as shown by the packing of the thread in the capsule, allows us to see the left/right asymmetry of the cells i.e. the direction in which the cells are facing when they have

their nematocysts pointing outwards. Because of the conspicuous nature of the nematocysts one can observe them in the living animal. This advantage is enhanced by the fact that patterns of cnidoblasts in siphonophores form very rapidly – with a microscope one can watch it happen.

Geometrically striking arrangements of nematocysts in siphonophores were depicted by Thomas Henry Huxley in his Ray Society Monograph of 1858 and by Keferstein & Ehlers (1861), but neither they, nor, so far as I can discover, anyone else has studied how these patterns are set up. Semal-van Gansen (1954) speculated that, in hydra, the arrangement of nematocyst types around a central stenotele was based on cell size. She implied that as the battery cell flattened down on the cnidocytes during growth of the tentacle, mechanical factors distributed the nematocysts appropriately.

On the other hand, Wood & Novak (1982) and Novak & Wood (1983) suggested that the developing cnidoblasts in hydra migrate to preordained places associated with the battery cell. They showed that a unique junctional complex forms basally between the cnidoblast, battery cell and mesogloea; even in the absence of cnidoblasts, a structure that may be equivalent to the junctional complex can be found. They suggested that these hemidesmosome-like sites are the predetermined places for cnidoblast attachment. In this article I describe a completely different mechanism that appears to operate in siphonophores. More details of this process will be published in Skaer (1987a & b).

Here I will describe some of the cell patterns that occur in siphonophores and I will summarize some of the contributions to setting up the patterns made by cell migration, by the cell sorting that occurs during and as a result of migration, and by the repositioning movements of adherent cells. The latter result in alignments or realignments of the adherent cells which then may be followed by synchronised but rapid changes in orientation and relative positions of the cells involved. These relative movements I call 'contact reassortment' (Skaer 1987a,b). They may involve the relocation of the whole cell, or just changes in the relative orientation, alignment or rotation of the cells about their axes. They represent a novel form of cell behavior that may perhaps be regarded as a series of stereotyped cell 'dances', distinct from, say, contact guidance or contact inhibition of movement (Abercrombie, 1970). These movements result in further cell sorting and the formation of cell rows (and in some cases the merging of rows to form longer rows that may be made up of different types of cell). From the shapes of the cell clumps built up by migration one can speculate about the precision of the cnidoblast navigation, the information required by different mechanisms of pattern formation, and the stages that might require positional information.

## RESULTS

### *a. Cnidosac patterns*

Mature nematocysts of most siphonophores occur only in knobbed structures on the tentacles called cnidosacs (Fig. 1a). Within each cnidosac they form five major patterns (Fig. 1b):

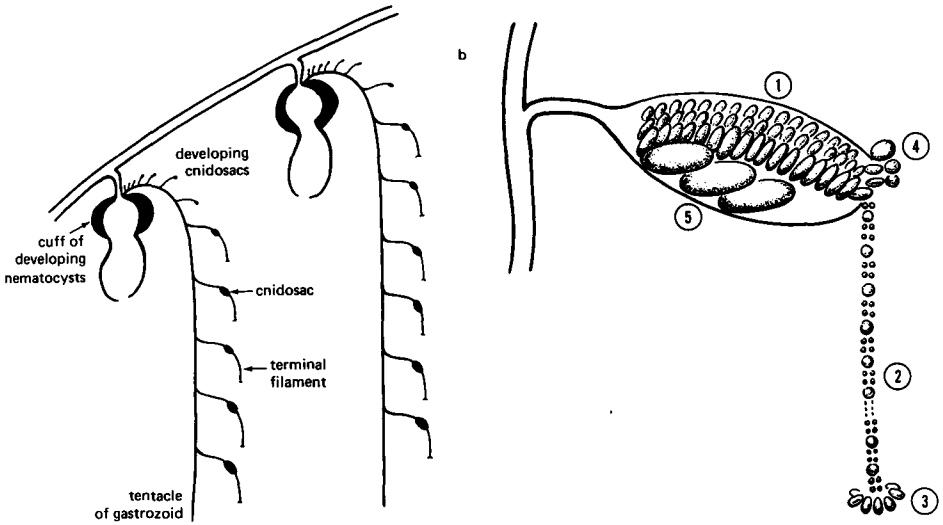



*Fig. 1a. Diagram of a typical arrangement of gastrozoids in a siphonophore, with each gastrozoid having one tentacle. The tentacle grows near its site of insertion on the gastrozoid and the cnidosacs form from outpushings of the tentacle. The cnidosacs are filled with cnidoblasts that have originated in the thick cuff around the top of the gastrozoid and then migrated into those cnidosacs that are at an appropriate stage of differentiation. Thus, the single tentacle represents a 'frozen' time sequence in the development of cnidosacs and their nematocyst patterns (youngest cnidosac proximally; oldest distally i.e. at the free end of the tentacle). Formation of the patterns is normally complete in cnidosacs a few millimetres down the tentacle.*

*Fig. 1b. Diagram of a typical Calycophoran cnidosac showing dorsal cnidoband (1); terminal filament (2); sinker (3); dorsal array of desmonemes (4); large lateral microbasic mastigophores (5).*

1. Cnidoband. This is a large array of anisorhizas that only differ from each other in size, if at all. The nematocysts form a wide band of highly aligned nematocysts that occupies most of the dorsal surface of the cnidosac. In *Calycophorae* such as *Chelophyes*, *Lensia* and *Abylopsis* the cnidoband nematocysts are arranged in seven straight rows, in *Forskalia*, 14 rows and in *Physophora* multiple rows – at least 19.
2. Terminal filament. The terminal filament is a thin, highly contractile filament attached to the distal end of the cnidosac. It contains two types of nematocysts only: rhopalonemes and desmonemes. In the genera considered here in detail (*Chelophyes & Abylopsis*) the arrangement of these nematocysts is a linear pattern whose repeat unit is 2 rhopalonemes, 1 desmoneme, 2 rhopalonemes. This pattern may be repeated 60–70 times along the terminal filament (Fig. 1b, 2, 3). In other genera (e.g. *Hippopodius*, *Forskalia*) the repeat unit is 2 rhopalonemes, 2 small desmonemes, 2 rhopalonemes (Fig. 4).

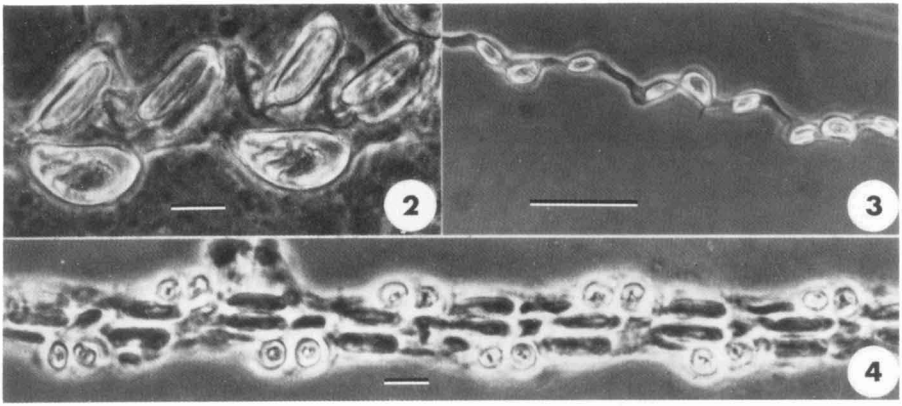



*Fig. 2. High power photomicrograph of a slightly squashed terminal filament of* Abylopsis *showing the paired rhopalonemes on each side of the (larger) desmoneme. Two repeat units are shown of the pattern 2 rhopalonemes, 1 desmoneme, 2 rhopalonemes. Phase contrast. The scale bar represents 10 μm.*

*Fig. 3. The same extended in vivo. The scale bar represents 100 μm.*

*Fig. 4. Terminal filament of* Forskalia *showing the repeat unit 2 rhopalonemes, 2 desmonemes, 2 rhopalonemes. Note that the relative size of the desmonemes in this genus is much smaller than in* Abylopsis. *Phase contrast. The scale bar represents 10 μm.*

3. Sinker. This is a circular disk containing large desmonemes only, situated at the distal end of the terminal filament.
4. Dorsal array of desmonemes. This pattern occurs at the distal end of the cnidoband near the origin of the terminal filament. It consists of large desmonemes similar to those on the sinker.
5. Lateral large nematocysts (usually microbasic mastigophores or stenoteles). These occur in fixed numbers (three on each side of the mature cnidosac in *Chelophyes*; eight on each side in *Abylopsis*). This pattern is ideal for studying the supply of cnidoblasts to the cnidosacs; individual nematocysts are large and their numbers are small. The numbers of nematocysts can be compared on the two sides of the cnidosac as well as in the cnidosacs immediately above and below.

*b. Accuracy of cnidosac patterns*

Cnidosac patterns are composed of cnidocytes that adhere to each other and in which the nematocysts are very highly oriented, not only with respect to the surface but also with respect to each other. This allows nematocysts of the same type to be compared in identical orientation. From this it is clear that the pattern of packing the tubule in the capsule follows the same course in nematocysts of the same type. In, for example, the large mastigophores of *Physophora* (Fig. 5) the thread emerging from the shaft immediately reverses its direction and moves forward towards the operculum on the right hand side of the shaft, it crosses above the shaft and when

approximately 3/4 of the way along the shaft it forms two large loops. These loops are on the upper side of the shaft and the anterior part of the second loop on the righthand side is the part of the tubule nearest the operculum. The remaining tubule forms loops beneath the shaft moving progressively to the rear of the capsule.

The invariance of cnidoblast pattern and orientation and the precision of construction of the nematocysts within the pattern is well shown in the cnidoband of *Physophora* (Fig. 6). The loops of tubule in optical section occupy identical places in all the nematocysts shown.

The numerical accuracy of the large nematocysts in pattern 5 has been mentioned and the precise repeat unit in the terminal filament and the manner of its formation is described in detail in Skaer (1987b) and will be summarized later in this article.

*c. The source of the cnidoblasts that form the patterns*

In siphonophores, all cnidoblasts develop in a conspicuous cuff, many cells thick, that is situated at the top of the gastrozoid (Carré, 1972; Skaer, 1973). Unlike the situation in hydra where developing cnidoblasts are linked by cytoplasmic bridges so the progeny of a stem cell form a nest (Fawcett, Ito and Slautterback, 1959; Fujisawa and David, 1981); daughter cnidoblasts in siphonophores do not remain in contact during development; they merely remain moderately close (Skaer, 1973). Moreover it is very difficult to see any topographical ordering of type or developmental stage in the cuff. Cnidoblasts of all types and states occur cheek-by-jowl. From this source, a primary sorting out occurs by the migration of individual cnidoblasts out of the gastrozoid and into the developing cnidosacs; a distance of 1–2 mm.

*d. Migration*

Enormous numbers of cnidoblasts migrate, initially along a broad common pathway, then into separate pathways leading to the 3–7 cnidosacs that are being filled at any one time. There is no obvious separation into types in these pathways nor in the stalks that lead to the cnidosacs, but in the cnidosac the anisorhizas of the cnidoband move along the *dorsal* surface, whereas the rhopalonemes together with all the desmonemes whether destined for terminal filament, sinker or dorsal array of desmonemes, move *ventrally* along the cnidosac. The large desmonemes of the dorsal array finally move dorsally at the end of the cnidosac. There is clearly some sorting into types in those cnidobands where there is a variation in size of nematocysts. (e.g. *Chelophyes* and *Abylopsis*) since each row contains nematocysts of a particular size only, but it is not yet clear whether this happens during migration. Nor is it clear at what stage the sorting of the large nematocysts of pattern 5 into right-&-left hand clumps occurs. It is clear that very few cnidoblasts migrate back down the stalk of the cnidosac. Saturation of the pattern with excess cells as shown by the withdrawal of the superfluous cnidoblasts down the stalk does not occur to a significant extent.

*e. The end of migration*

Migration ends with the cells sorted into identical types that form adherent clumps (Skaer, 1987a,b). Unpublished work with Dr. A. Spencer has shown that the

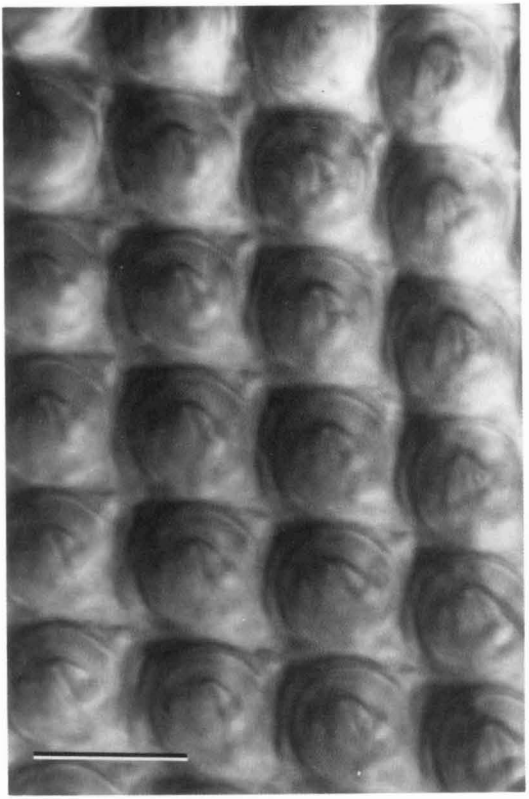


*Fig. 6. Cnidoband of* Physophora *seen from above. Four rows of cnidoblasts run from top to bottom of the picture in what is virtually a square lattice pattern. The geometrical precision of the pattern, the invariant orientation of the nematocysts within the pattern and the identical packing of thread within the capsules are shown. Nomarski optics. The scale bar represents 10 μm.*

cnidoblasts in the clumps are dye coupled for Lucifer yellow throughout all the subsequent movements of pattern formation. The end of migration is signalled by the rotation of the nematocyst through 90° so it comes to lie normal to the surface. The clumps form in the appropriate areas for pattern formation but are often of rather indefinite shape; for example a large, approximately helical clump of rhopalonemes

*Fig. 5. Large mastigophores of* Physophora *showing the invariance of orientation of the nematocysts and the similarity in packing of the shaft and tubule in the capsule in these identically oriented nematocysts. These nematocysts are approximately 180 μm long. Nomarski optics. The scale bar is 10 μm.*

and a rather smaller, approximately helical clump of small desmonemes form in the anlage of the terminal filament (Fig. 7, 8, 9). Further building of the patterns in the cnidoband and the terminal filament is described in more detail in Skaer (1987a,b) and will be summarized here.

In the cnidoband of *Physophora*, where all cnidoblasts are identical, an initially hexagonal packing of the adherent cnidoblasts in a clump is transformed into rows having a square lattice arrangement. Row formation is associated with rotation of the nematocysts (possibly of the cnidoblasts?) about their axes normal to the surface so

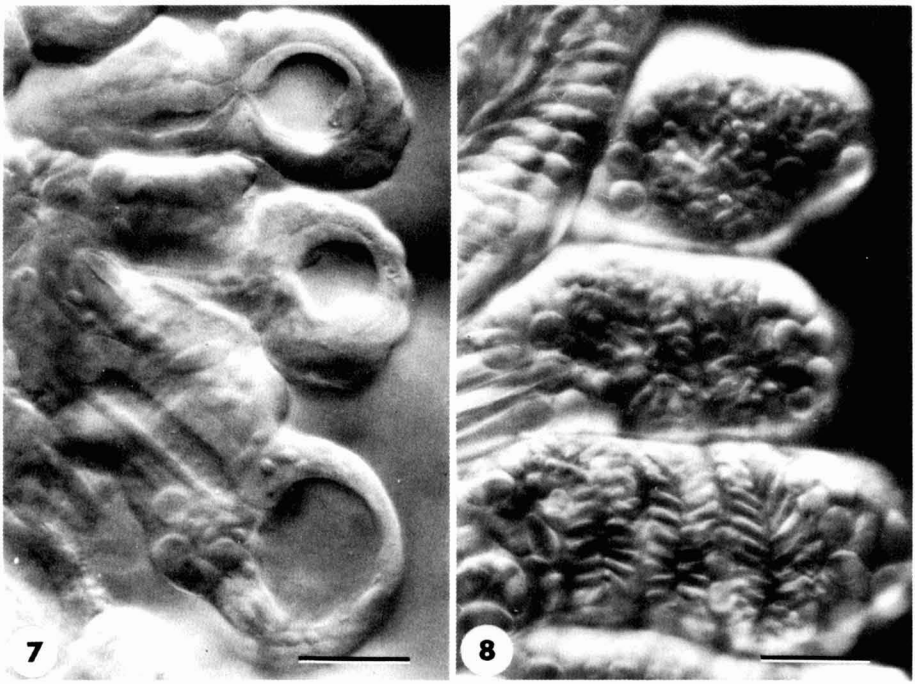



*Fig. 7. Three developing cnidosacs of* Chelophyes. *The lowermost one has just started to fill with cnidoblasts. The spherical anlage on the right-hand side are the precursors of the terminal filament. Nomarski optics. The scale bar is 100 μm. Reproduced by permission of The Company of Biologists Ltd.*

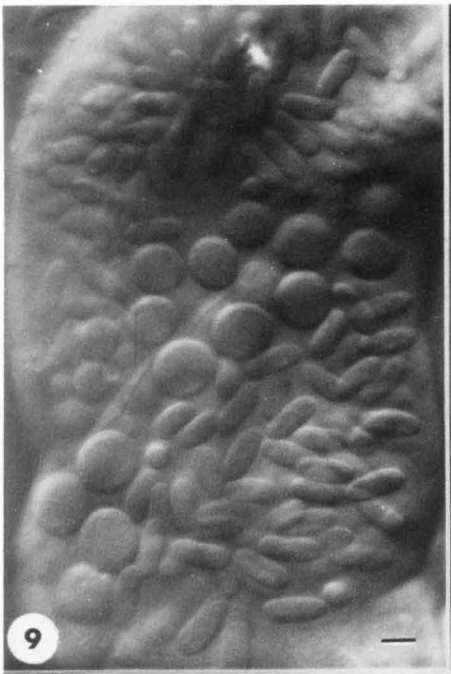
*Fig. 8. Three developing terminal filaments of* Chelophyes *at different stages of filling with cnidoblasts. The earliest stage (at the top) shows an irregular clump of small, cigar-shaped rhopalonemes flanked by a small number of spherical desmonemes. In the middle filament the rhopalonemes have formed a clump of two helical gyres in which the cells are arranging themselves into rows even though filling is not complete. In the bottom terminal filament the clump of rhopalonemes has been transformed into three helical gyres interspersed with desmonemes. The herring-bone pattern within each gyre is due to row formation and the merging of rows. The clump of large desmonemes at the far right-hand side will form the sinker. Nomarski optics. The scale bar is 100 μm. Reproduced by permission of The Company of Biologists Ltd.*

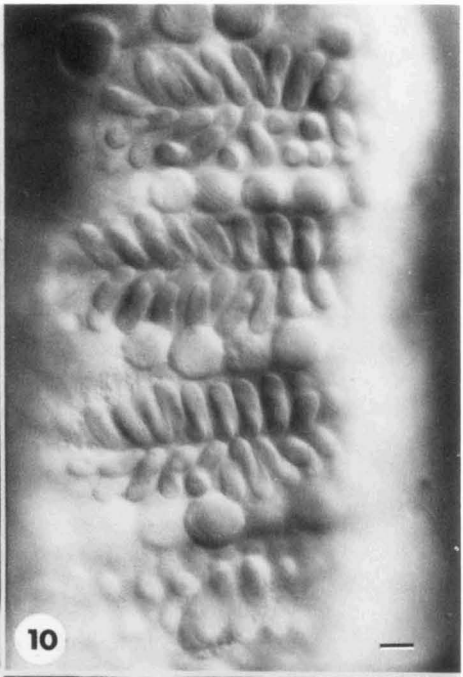
they coincide exactly with the orientation of neighbors. Row formation is fundamental to pattern-building in siphonophores. Row formation in the cnidoband of *Chelophyes* and *Abylopsis*, where the cnidoband nematocysts are all the same general type but differ in size, is more complex. Each row contains nematocysts of one particular size class. Sorting within the clump by a side-to-side pendulum movement of the cnidoblasts is aided by a certain precision of migration. Thus the cnidoblasts of the small anisorhizas that lie in the outermost row on each side of the cnidoband migrate near to the edge of the band of migrating cnidoblasts in the stalk of the cnidosac. Similarly the larger anisorhizas, that form a row on each side next to the smallest, do indeed tend to end their migration towards the edge of the cnidoband. It is not clear how the left-right symmetry on either side of the three rows of medium-sized anisorhizas is set up. Despite this relative accuracy of migration in building the cnidoband, cell sorting of adherent cells is a major factor in the precision of the procedure. The pendulum-like movements in directions at right angles to the forming row take place after migration, i.e. within the adherent clump. The movements cannot be given a periodicity since some nematocysts remain obliquely oriented until row formation is complete (Skaer, 1987a). The nematocysts may depart up to 45° from their post-migration position (normal to the surface). It is assumed that some form of differential adhesion in this position achieves this sorting. After the pendulum movements have stopped and the nematocysts again lie normal to the surface, the row is a zig-zag arrangement whose members progressively align themselves as row formation proceeds from the distal end of the cnidoband (Skaer 1987a)

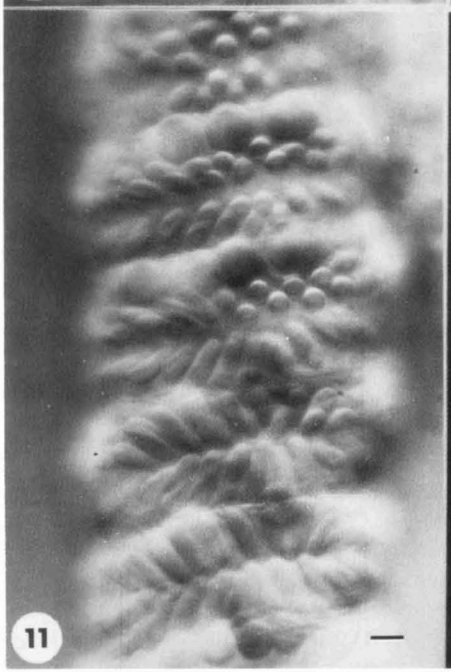
Row formation and the pendulum-swinging at right angles to the row are particularly apparent in the terminal filament. Formation into the four rows of rhopalonemes and one row of desmonemes precedes the one-way pendulum maneuver that merges row with row (a type of reverse sorting) (Fig. 10, 11, 12, 13). The simultaneous merging of two distal rows of rhopalonemes and of two proximal rows of rhopalonemes effectively doubles the length of the filament which then undergoes a further elongation as the resulting two rows of rhopalonemes merge with the row of desmonemes to give the final repeat unit 2 rhopalonemes; 1 desmoneme; 2 rhopalonemes that is found in *Chelophyes*, *Abylopsis* and *Lensia* (Fig. 13). In the mature filament each repeat unit is separated from its neighbor by a length of contractile filament approximately equal to half a repeat unit. As this final elongation and merging of unlike rows occurs, the terminal filament which hitherto had been helically coiled, collapses into a long and highly contractile filament. In genera such as *Hippopodius* and *Forskalia* where the repeat unit is (2 rhopalonemes; 2 desmonemes; 2 rhopalonemes)$_n$ (Fig. 4) the paired desmonemes are smaller than in *Chelophyes* and are derived from two rows per gyre rather than the one as described above. The regularity of the repeat unit would appear to depend in part on the relative spacing of the cells in the rows.

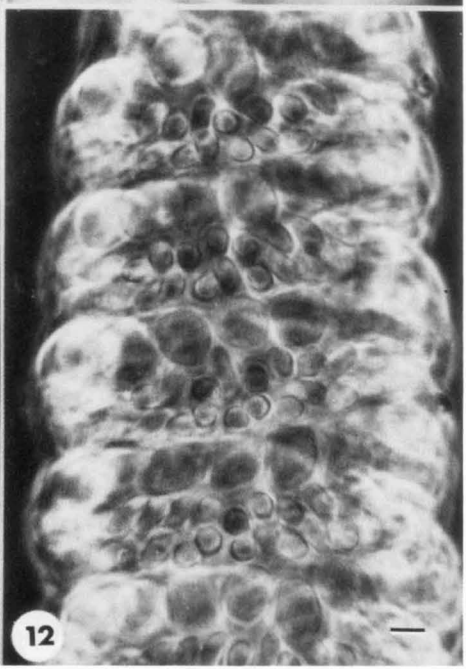
## DISCUSSION

The results show that in siphonophores the patterns are not built by direct migration to particular sites, rather, migration builds clumps of identical cell types in


9


10


11


12

particular areas. In other words migration sorts cells into specific categories of cnidae (or nematocysts). Migration also appears to provide the clump with the correct number of cells. After migration, when the cells are adherent and dye coupled, they then perform the remarkable sorting, aligning and interacting behavior patterns that control the detailed placing of the cells. Elsewhere (Skaer, 1987b) I have called these maneuvers 'contact reassortment' to distinguish the movements of cells in contact (and dye-coupled) from the locomotion of migrating cells. The placement of cells by 'contact reassortment' is both geometrically and numerically invariant. This exactitude depends on precise alignment of the cells into rows, precise control of cell size (or, effectively, cell spacing) and the precise orientation of the cells within the rows with respect to their intrinsic asymmetry. This asymmetry is expressed, for example, in the exact orientation of the nematocysts about their longitudinal axis – an asymmetry that is revealed only because of the precision of construction of the nematocysts themselves.

We do not know whether the migrating cnidoblasts need or have positional information continuously available; it could be that all cells of a particular type arrive in a clump simply because all have identical navigational instructions. In the case of the adherent cells, however, alignment into rows, the intermeshing of the rows and the subsequent rotation through 180° of cells from one row to face in the same direction as the row they have entered, would seem to require the cells to know where they are in the pattern and, therefore, the direction they should be facing. Although one could envisage that identical cell types could develop identical cell surface patterns of adhesion, with cells adhering in a straight line by self-assembly, rather like LEGO bricks snapping together to build a straight row, the fact remains that this would still require one cell – the 'founder' cell – to be correctly oriented so it would

*Fig. 9. Higher power view of a developing terminal filament of* Ablyopsis *at a stage corresponding to that in the top anlage of Fig. 8. Two gyres of the helical clump of rhopalonemes are traversed by the oblique clump of spherical desmonemes. These are small desmonemes but are nevertheless substantially larger than the rhopalonemes. At this stage cnidoblasts of both types are still entering the terminal filament. Nomarski optics. The scale bar represents 10 μm.*

*Fig. 10. Terminal filament of* Abylopsis *showing later stage with four gyres of the helically coiled filament. Within each gyre are four rows of rhopalonemes and one row of desmonemes. The two proximal rows are merging with each other as are the two distal rows giving rise to the herring-bone pattern. This corresponds to the bottom filament in Fig. 8. Nomarski optics. The scale bar represents 10 μm. Reproduced by permission of The Company of Biologists Ltd.*

*Fig. 11. Terminal filament of* Abylopsis *at a slightly later stage showing the zig-zag positioning rhopalonemes as the two pairs of rows merge to produce two rows per gyre. The depth of each gyre is thus reduced and the length of the filament increased. Approximately five gyres are shown. Nomarski optics. The scale bar represents 10 μm.*

*Fig. 12. Terminal filament of* Abylopsis *at an even later stage. There are now only two rows of rhopalonemes in each gyre and the gyres have diminished in depth still more. The filament has increased correspondingly in length. Phase contrast. The scale bar represents 10 μm.*

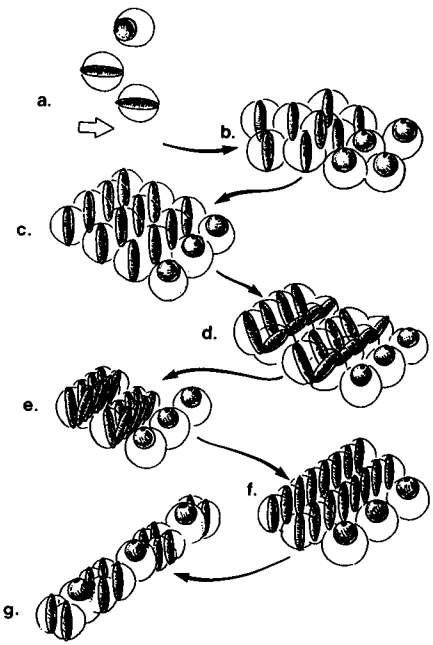



*Fig. 13. Diagram showing the formation of the pattern of nematocyst types in the terminal filament of* Chelophyes *or* Abylopsis.
*a. Cnidoblasts migrate to the site of pattern formation, nematocyst and operculum trailing. The open arrow indicates the direction of migration.*
*b. Formation of clumps of identical types of cell at the site of pattern formation. This marks the end of migration – nematocyst normal to surface, operculum at the surface. Compare with Fig. 9.*
*c. Row formation within the clump of adherent cells. Four rows of rhopalonemes (3 shown here) and one row of desmonemes formed.*
*d. Merging of rows of rhopalonemes – compare with Fig. 10 and the herring-bone pattern in Fig. 8.*
*e. Later stage of merging, with rhopaloneme orientation returning nearly normal to the surface and forming two long zig-zag rows from four shorter straight rows. Compare with Fig. 11.*
*f. Later stage still – only two long rows of rhopalonemes alongside the single row of desmonemes. Compare with Fig. 12.*
*g. Mature terminal filament – merging of unlike rows after a process similar to that in d. to form the repeat unit 2 rhopalonemes, 1 desmoneme, 2 rhopalonemes. Compare with Fig. 2.*

initiate correct orientation of the row. It is perhaps simpler to assume that all cells have this positional information.

Building a pattern cell-by-cell by the mechanism of migration (Wood & Novak, 1982; Novak & Wood, 1983) is an essentially *serial* activity requiring large amounts of information to be fed back to the migrating cells. The type of pattern building that occurs in the terminal filament proceeds simultaneously and in parallel throughout the pattern. It is thus a very rapid way to build a pattern. In some genera, the construction of the cnidoband proceeds sequentially but is not dependent upon particular cell types arriving at particular times, or on cells finding and binding to preordained sites. Migration to the cnidoband appears to carry out an approximate sorting, so the smallest anisorhizas arrive towards the edge of the pattern, and the medium sized ones in the centre. It is not yet clear whether migration, or a cell sorting procedure preceding migration, or a possible right/left distribution of daughter cells (Albrecht-Buehler 1977a,b; Levinstone, Eden & Bell, 1983) allocates identical cell types to the two sides of the cnidoband.[1] Investigations into this are proceeding with the large microbasic mastigophores on each side of the cnidosac of *Chelophyes*.

It is tempting to regard the mechanisms described here as general mechanisms in animal development, that have been observed in siphonophores because of the exceptionally favourable circumstances. Nevertheless, one must not forget that siphonophores are creatures that grow very rapidly (Biggs, 1976) and some of the mechanisms may be related to this. However, rapid and accurate formation of patterns is often a general feature of developing systems, whether in embryos or adults.

## ACKNOWLEDGMENTS

This work was financed by grants from the Royal Society of London (Marshall & Orr Bequest & Browne Research Fund). I thank the Director and Staff of the Station Zoologique, Villefranche-sur-Mer where this work was performed. The Drs. Carre and Cosson were particularly kind and helpful. Dr. A. Spencer carried out the Lucifer yellow dye coupling experiments while we were at Villefranche.

Figures 7, 10 and 8 are reproduced with permission of The Company of Biologists Limited.

[1] It does not seem that the latter is a likely explanation for all cases of handedness described here – it cannot account, for example, for the odd number of rows (7) in the cnidoband of *Calyphorae*.

## REFERENCES

Abercrombie, M. 1970. Contact inhibition in tissue culture. *In vitro* 6:128–142.

Albrecht-Buehler, G. 1977a. Daughter 3T3 cells: are they mirror images of each other? J. Cell Biol. 72:595–603.

Albrecht-Buehler, G. 1977b. The phagokinetic tracks of 3T3 cells. Cell 11:395–404.

Biggs, D. C. 1976. Nutritional Econology of *Agalma okeni* (Siphonophora: Physonectae) In G.O. Mackie (Ed) Coelenterate Ecology and Behaviour pp.201–210. Plenum Press, New York & London.

Carré, D. 1972. Etude du developpement des cnidocystes dans le gastrozoide de *Muggiaea kochi* (Will, 1844) (Siphonophore calycophore). C.r. hebd. Seanc. Acad. Sci., Paris. 275:1263–1266.

Fawcett, D. W., Ito, S. & Slautterback, D. 1959. The occurrence of intercellular bridges in groups of cells exhibiting synchronous differentiation. J. biophys. biochem. Cytol. 5:453–460.

Fujisawa, T. & David, C. N. 1981. Commitment during nematocyte differentiation in *Hydra*. J.Cell Sci. 48:207–222.

Günzl, H. 1979. *Dipurena reesi* (Hydrozoa) Wanderung der Cnidoblasten in den Rhizostolonen. In G. Wolff (ed.) *Encyclopaedia Cinematographia* pp.1–15 Film E 1106/1966. Institut für den Wissenschaftlichen Film, Göttingen.

Huxley, T. H. 1858. The Oceanic Hydrozoa; a description of the Calycophoridae and Physophoridae observed during the voyage of H.M.S. 'Rattlesnake' in the years 1846–1850. Plate V. The Ray Society, London.

Keferstein, W. & Ehlers, E. (1861). *Beobachtungen über die Siphonophoren von Neapel und Messina. Zoologische Beiträge gesammelt im Winter, 1859–1860 in Neapel und Messina* pp.1–34. *Wilhelm Engelmann, Leipzig.*

Levinstone, D., Eden, M. & Bell, E. 1983. Similarity of sister-cell trajectories in fibroblast clones. J.Cell Sci. 59:105–119.

Novak, P. L. & Wood, R. L. 1983. Development of the nematocyte junctional complex in hydra tentacles in relation to cellular recognition and positioning. J. Ultrastruct. Res. 83:111–121.

Semal-van Gansen, P. 1951. Le cnidosome de l'hydre et le bouton urticant. Bull. Acad. roy. Belgique Sci. 53 ser. 37: 650–664.

Skaer, R. J. 1973. The secretion and development of nematocysts in a siphonophore. J. Cell. Sci. 13:371–393.

Skaer, R. J. 1987a. The formation of cell rows. A study of the cnidoband of siphonophores. Submitted to 'Development'.

Skaer, R. J. 1987b. A cell sorting procedure in pattern formation. The terminal filament of siphonophores. Submitted to 'Development'.

Wood, R. L. & Novak, P. L. 1982. The anchoring of nematocysts and nematocytes in the tentacles of hydra. J. Ultrastruct. Res. 81:104–116.