Ontogetic development of clour patterns

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two patterns may even be differently coloured. In *Oliva porphyria* L. we have what might at first seem to be a similar situation, wherein numerous undulous transverse lines correspond near the top of the whorl to the much fewer zigzagging-ones of the «tent» pattern over the rest of the shell surface (Pl. XI, fig. 9). The transition is here however somewhat less abrupt than in the preceding case; and on closer look it is seen that whereas about half of the undulous lines are the continuation of the zigzagging lines of the surface «tent» pattern, the other half is connected to another pattern, very similar to the surface one, but «buried» deep in the shell substance: this second pattern «emerges» near the whorl top presumably because the shell wall is very thin there. Periodicity from the two patterns is thus combined here, and there is no real change in that respect, as a period on the upper region of the whorl still corresponds to a period on the main part of the whorl, if the total pattern is taken into account. A real change in periodicity, however, occurs in this form at the very top of the whorl, where the transverse lines bunch up into only a few units: just below the suture there is often no secretion of elements at all.

In *Nautilus pompilius* L., the period is much shorter at the center than at the sides, but here the transition is very gradual.

In *Neritina oualanensis* Lesson we often have sharply alternate zones of short-period elements and long period ones (Pl. V, fig. 16); in «tented» patterns, such as those of *Oliva porphyria* L., some «tents» are much vaster than others: to produce such larger features would obviously take a much longer time, or period, than to secrete the smaller neighbouring «tents» and as various sized «tents» are distributed rather irregularly on the whorl, so are the periods of secretion (Pl. VI, fig. 10). Finally in the pattern of *Conus textile* L. we have in some parts of the shell the irregular periodicity of the «tented» pattern, and in others the more regular one of the transverse undulous lines.

V. Ontogetic development of colour patterns

A. Introduction

The figures illustrating this chapter are extremely schematized and compressed (in the proximal-distal direction) diagrams of the pattern of an unrolled shell: these examples have been selected to give an idea of the rather forbidding variety that is to be found in these ontogenetic developments of patterns. In the almost total absence of juvenile shells in the collections, it was possible to diagram pattern ontogenies only for the whorl sides (=above the suture line). As can thus be seen, the pattern changes are so different from one group (family, genus and even species) to the other that most often an inter-group comparison of such phenomena appears rather futile.

Some examples of variety in pattern ontogeny may be cited:

Patterns may appear early in the life of the shellfish (at the end of the first whorl in *Tricolia pullus* L. for ex.), or relatively late (only after several whorls in *Charonia tritonis* L., unless the homogeneous suffused pink colouring of the juvenile shell is counted as «pattern»; and very far from the apex, in *Sunetta meroe* L., etc.). Patterns may appear at once with maximal, or almost maximal colour intensity (*Sunetta meroe,* etc.) or as very faint features, with subsequent gradual increase in colouration (*Pyramidella maculosa* Lam., *Liguus blainianus* Poey, etc.). Patterns may appear fully developed, or almost so (*Sunetta meroe* L., etc.), or may change later on. These changes may involve additions to, substractions from, or modifications of the initial pattern, or various combinations of all of these.

In the case of addition of new elements, this may occur without appreciable modifications of the elements already there, producing a more complex pattern (in some *Smargadia viridis* L., addition of black lines on a white-blotched pattern), or a more intricately organized one (the appearance of connective lines between the zigzags will lead to formation of a hexagonal network, Pl. I, fig. 7, vs. 10 and 13): these new elements may, on the other hand lead to, or in some way provoke modifications in the original pattern elements (the addition of white blotches in *Tricolia pullus* appears somehow to be involved with the formation of lines joining the spots distal from them; the cells of the juvenile network of *Bulla striata* Brug. become highly modified by addition of pigment where the blotches of the adult are added. And as indicated below, the addition of red pigment in some adult *Tricolia pullus* may lead to the greatest possible change, the total elimination of the original pattern, and indeed of all pattern as such). Changes in the original pattern may finally occur more or less simultaneously with the addition of new units, without the latter event being necessarily related to the first (appearance and disappearance of bands in *Vexillum vittatum* Swains.).

Changes in pattern and pattern elements may occur by fractioning these patterns or elements into new ones (realized in different ways in *Mitra mitra* L., *Neritina communis* Quoy var., and some undetermined *Umbonium,* etc.); by emphasizing some part of the former pattern (as in the formation of the rims of the bands of *Liguus blainianus* Poey); by changes in the shapes of these former elements (as for the transverse bands in *Liguus blainianus*) etc.

We may on the other hand return to the primitive pattern by reversing all the change processes mentioned above (red zones disappearing in the last whorl of some *Neritina communis* Quoy, blotches and lines disappearing in the adult pattern of some *Tricolia pullus* L., etc.).

Finally we may have patterns with their greatest complexity in very early stages, as in some *Smaragdia viridis* L. which have lines and blotches in the early juvenile stages, and a homogeneous green coloration in the adult.

Other things may be learned from an examination of pattern ontogeny. An important one is that similar features may be produced in different ways (a kind of «convergence» in development). The case of the networks has been discussed earlier (p. 29). Radial alt. c. bands may be produced: (1) From rows of spots, by addition of pigment along the width of each row (as in *Liguus blainianus* Poey, Pl. V, fig. 4); (2) from rows of spots, by addition of pigment between the rows, so that the colourless portions of the rows are brought out (as in *Natica canrena* L., Pl. V, fig. 5); (3) from dark homogeneous radial bands, by the addition of periodic white blotches (as in *Turbo petholatus* L., Pl. V, fig. 6); (4) by radial fractioning of a homogeneously transversely striped pattern (as in *Neritina communis,* Pl. V, fig. 7); (5) from various other pattern features, such as lobes set behind each other, as in *Neritina oualanensis* Lesson, etc.

An examination of pattern ontogeny may also furnish explanations for strange or intricate types of pattern hard to understand from a mere examination of the adult whorls. Such is the case for the «confused» pattern of the adult of *Bulla striata* Brug. or the networks of *Strombus vittatus* L. The adult pattern of a most common variety of *Neritina communis* Quoy (Pl. IX, fig. 1) is at first sight very straightforward: radial alt. c. bands with alternate black and white stripes separated by zones of uniform red coloration. Closer examination of these red zones in a number of specimens reveals, underlying this apparent simplicity of pattern, the presence of some disturbing factor: for sometimes the red colour of the zones shows a vague striping; at other times there appear in the middle of the zones islands of black and white stripes like that found in the alt. c. bands; and finally stripes from the bands may here and there invade the red zones. Observation of the juvenile whorls shows that the striped pattern of the bands originally covered the whole side of the whorl (see Pl. IX, fig. 1), the red zones forming only later: it is apparent therefore that in the latest growth stages of the shell, the juvenile pattern tends to reassert itself in the red zones after a long interval of suppression, and in some specimens like that figured (at c) this reassertion may become complete.

B. Examples of pattern ontogeny

In *Bulla striata* Brug. the earliest pattern is very difficult to observe on account of its indistinctness and the translucency of the shell. It appears made up of alt. c. bands with short brown (at first only translucent) and much longer opaque white portions. Somewhat later brown wavy transverse lines appear that apparently cross the alt. c. bands, connecting the brown portions of one band with those of the next. When these lines are close together we will have formation of a hexagonal network (Pl. VI, fig. 20) [44]. In later growth stages a blotched pattern appears that partially replaces this peculiar hexagonal network. Between the dark blotches, or areas of heavy secretion, the network is variously suppressed or dimmed. Where pigment is added it may: (1) Enlarge or darken the brown alt. c. band portions; (2) fill some cells; (3) in places fill everything except isolated cells or

[44] Where the bands are very narrow, the brown portions may assume a rectangular shape, and become the junction spots of a more or less rhombic network.

even central portions of such cells; (3) eliminate all trace of the network, producing a homogeneous brown area. The end result of these processes is a pattern which may well be termed «confused» [45].

In most *Tricolia pullus* L. (Pl. VIII, fig. 3) the pattern begins as a few brown dots or spots rather irregularly arranged (3, right). There is later an apparition of one or more elongate white opaque blotches, arranged transversally, which, to all evidence, cause the brown spots at their distal side to fuse into a sinuous transverse line. Two or three rows of spots form distally from this line and apically from the next set of blotches (3 center); this pattern is then periodically repeated. In the adult various modifications to this juvenile pattern may be produced, such as follow: (1) The white blotches and associated lines may disappear and the pattern will return to one of dots, as in the earliest juvenile stages: here however the dots will be aligned most often in two or even three directions (see p. 21); (2) as in the preceding, but with lines joining the dots in any one of the three directions mentioned, this direction being emphasized at the expense of the others; (3) lines may join the dots in both oblique directions at once, forming a rhombic regular network. The network lines are faint in all the present specimens; (4) The rows of white blotches and associated sinuous lines, instead of vanishing, may appear with much greater frequency, to the extent of eliminating all other elements; (5) addition of red or brown pigment my gradually efface part or all of the pattern (fig. 3, left) [46], etc.

In *Mitra pontificalis* Lam. and *M. mitra* L. (Pl. VIII, fig. 2), the juvenile whorls are orange-red, with white transverse (or concentric) bands mostly situated on «prolabral» swellings which occur on the distal side of growth breaks. Later the red «ground» becomes gradually split up into very distinct rectangles, except for a few extensive irregular blotches with blurred boundaries, that appear locally near the suture line of the adult.

The pattern of *Liguus blainianus* Poey was observed all the way from the protoconch on (Pl. VIII, fig. 1). We have at first a dark protoconch not clearly differentiated from the rest of the shell. The dark protoconch colour maintains itself on the top of the succeeding whorl, the rest of that whorl being of light orange hue. Transverse brown bands then appear which soon become restricted to the middle of the exposed part of the whorl, while the orange ground vanishes. Yellow coloration is then progressively added to the radial zone defined by the upper and lower limits of the brown bands so that these become darker and the areas between the bands become tinted with yellow: we thus get a radial zone with brown and yellow portions: the yellow colour of the latter often darkens on the upper and lower limits of the band to form a «rim»; a similar rim appears

[45] Complications to this already complicated enough picture arise from the presence of dark radial bands that have a strong influence on the development of blotching, where they occur.

[46] The pattern development described pertains to the whorl sides only, the whorl bases not being visible in the available specimens.

below a dark radial band which has meanwhile formed just beneath the suture.

In *Liguus blainianus* Poey we thus have seen an originally transverse pattern gradually transformed into a mainly radial one through the following steps: (a) The extension or span of the successive transverse bands becomes reduced; (b) pigment is added along the radial zone thus defined, and (c) another radial, subsutural band is added.

In *Strombus vittatus* L., the pattern appears rather late as zigzagging lines in the interspaces of the transverse ribbing. As the ribs disappear, the zigzags become more highly irregular; connecting lines may appear between zigzags, as also intercalary zigzags which may join to the others; there results a more or less regular hexagonal to rhombic network.

Later, in the last whorl, this essentially transverse pattern may be partly replaced by a pattern with two components of opposite obliquity, which produces a more regular, entirely rhombic network (Pl. X, fig. 9).

The earliest observed whorls of *Vexillum vittatum* Swains. are entirely brown; a clear zone may appear on the middle of the whorl-side, with a dark line forming on each side thereof (Pl. VIII, fig. 4) and separating it from the upper and lower brown zones. In later stages the lower zone becomes light also, but the boundary line with the middle zone may persist almost to the adult stage.

In *Charonia tritonis* L. the earliest colouring observed near the apex is a homogeneous pink (with light beige varices); this pink colour vanishes slowly thereafter. There soon appears a pattern of broad transverse irregular brown bands; later on appears on the radial ribs (and especially where they are widest, just before the start of a varix) an alternated colour pattern, whose dark portion is composed of brown lobes facing distally: the boundary between dark and light portions is gradual on the proximal side of the lobes, abrupt on the distal side (Pl. X, fig. 3). The transverse brown bands also persist throughout, traversing or influencing in various ways the lobed pattern of the ribs.

In *Neritina communis* var. there appears first a homogeneous pattern of alternate black and white zigzagging transverse stripes (Pl. IX, fig. 1 A). Soon this pattern is literally split into radial bands by red wedges that develop into radial red zones intercalated between the bands (Pl. IX, fig. 1 B). This new pattern then, of alternating zones of red colour, and bands with alt. c. of black and white stripes, often persists to the end; there is however, often a tendency for the original homogeneously striped pattern to reassert itself at the end of the adult whorl, and the reappearance of this original pattern may be total in some individuals (Pl. IX, fig. 1 C).

In the pelecypod *Meretrix petechialis* Lam., var., the evolution of the pattern is extremely complex and moreover highly variable: the juvenile form shows an irregular transverse zigzag pattern on a white ground; soon appear big blotches of grey colour, which often have their origin in a zigzag, and then spread fan-wise and frequently coalesce to form a grey ground which tends to fade out distally. Except in the earlier juvenile stages the zigzags tend to form small brown blotches at their extremities, and in the adult stages these blotches, aligned in more or less transverse rows, are all that may be left of the earlier zigzag pattern (Pl. IX, fig. 2).

VI. Relation between colouring and sculpture

The relationship between colouring and sculpture on the Molluscan shells is extremely variable, and at times quite complex: Wrigley's statement (1947, p. 212) that «colouring and sculpture are conformable» can only be considered as a very general approximation of the truth, even if one were to extend the term «conformable» to include any apparent influence whatever of the ribbing on the pattern elements: and indeed, in the cases where these latter are not parallel to the ribbing, this one will usually have to be pretty sharp or strongly developed to have any significant influence. A more accurate version of that «law» would read thus: Colouring appears generally to show some relation to sculpture, or to be in some degree influenced by it.

Even though the relationship between colouring and sculpture may at times be vague or doubtful, there are numbers of cases where the colour patterning appears entirely controlled by, or conformable to, the sculpture; and in other cases where such conformability is not immediately apparent, the first is impossible to explain without reference to the second. *Charonia tritonis* and *Harpa major Röding* were mentioned by Wrigley as good examples of close conformity between colouring and sculpture, and indeed appear to be so in the adult stages at least. The situation might at first sight seem different in *Pyramidella maculosa:* the colouring here comprises two transverse components, one of numerous brown bands, the other of scarcer, more irregular, wider, and rather indistinct bands that make an angle with the first. Fine white radial lines cut through the narrow bands and deeply incise the wide ones (Pl. IX, fig. 3). No ribbing could be observed in any of the individuals examined here, not even in the juvenile stages. A closer inspection, however, reveals the presence on the inside surface of the shell of periodic denticulated swellings such as are normally found under varices. The denticles of the swellings are often continued between these structures by radial interior ribs. It may then be observed that the white radial lines on the outside of the shell correspond to these denticles and interior ribs; and that the indistinct dark bands are laid down in front of (= distally from) each swelling and probably at about the same time, and are thus secreted far inside the shell. To have tried to «explain» or describe the outside colouring without reference to the sculpture would in this case have been senseless, even though here the sculpture is not visible on the outside of the shell.

It appears that there are at least four main types or categories of relationship between colouring and sculpture: these are essentially the same that had already been mentioned by the author in 1966 (p. 237) when discussing the positions of denticles relative to ribs. These categories may be briefly summarized as follows: