

# Presumed activities of sources of secretion

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## II. Terminology

In the present work, which though it necessarily emphasizes the Gastropoda <sup>4</sup>, nevertheless includes examples from all three main classes of Mollusks, a unified terminology has been adopted for similar features in all the shells of that Phylum. The *radial* direction will denote a line traced from the summit of the cone of the Archetype Mollusk (or of *Patella*, or *Pecten*) to the margin of its shell (= radial direction in Pelecypods, spiral in Gastropods). The *concentric* «direction» is parallel to the growth lines. The *transverse* direction will as in Cox (1955) refer to a direction that is almost but not quite entirely concentric. — In many Gastropoda the colour pattern may be divided vertically into three zones: A. A *superior zone* above the shoulder, where the latter exists, or above where the shoulder would presumably be, if it does not exist, B. A *central zone*, covering the major part of the whorl, C. A *inferior zone* down from the fasciole. In some cases a thin zone (subsutural) may become differentiated at the very top of the whorl, below the suture. The portion of the whorl hidden by the succeeding whorl is referred to as *base of the whorl*, as in DAVIES (1935), that not hidden as the *side of the whorl*. — The terms «*distal*» and «*proximal*» are used as in BOEGGILD (1930) to denote respectively the direction away from or towards the apex of the shell. — *Light spots*, or *ocelli*, are here defined as colourless or light-coloured spots set in a darker ground: thus the ocellated pattern of *Nitidella ocellata* Gm. (see also Pl. III, fig. 7 b).

## III. Presumed activities of sources of secretion <sup>5</sup> (as deduced from the secreted patterns)

If we omit the Cypraeidae and assorted families, where the secretion organization is complex (it appears that most of the mantle surface is involved), and in any case where the resulting patterns have been studied in some detail (see ROBERTS, 1851), we may say that in general <sup>6</sup> the external coloration of all Mollusks is produced from the mantle edge, and indeed for most purposes may be considered as

<sup>4</sup> Only one family among the other Mollusca studied, the Veneridae of the Pelecypods, shows any great variety and complexity of colour pattern on its shells.

<sup>5</sup> «Source of secretion» (i. e., of colour secretion, it alone being considered in this work, unless otherwise indicated) is used for want of a better term. It does not imply any particular group of cells, only the locus or region whence the secretion comes; thus the expression «sources of secretion ambulatory» does not prejudice on what actually happens (whether the cells actually move or whether secretion shifts from one group of cells to the other — the more likely possibility).

<sup>6</sup> In general, but by no means always! In *Tellina radiata* L. for ex., the «rays» are produced well within the edge of the shell, and the yellow colouring only within the pallial line. The rays are brighter near the apex only because the shell is thinner there. In number of species (for ex. in Olividae such as *O. ispidula* L., in *Lioconcha castrensis* var., etc.), the

produced from a single line. It is then the varying activity and extent of the sources of secretion along this line that is responsible for all the patterns to be illustrated below. The possible types of activities are not many and are all evidently realized in some Mollusk or other:

### *A. Sources of secretion stationary*

(1) Continuous secretion, producing radial lines, bands, zones or homogeneously coloured shells, according to the width along which the secretion acts (Pl. I, fig. 1: A, E).

(2) Intermittent secretion, producing radial rows of spots, of lines, and concentric lines <sup>7</sup>, again according to the width along which this secretion takes place (Pl. I, fig. 1: B, C, D).

### *B. Sources of secretion ambulatory*

#### 1. Secretion continuous

a) Motion of sources constant. We have here the production of straight oblique lines and bands (Pl. I, fig. 1: F, G).

b) Motion of sources accelerating. This results in the production of curves of all types, whose regularity will depend on that of the acceleration (positive or negative) of the sources (Pl. I, fig. 1: H, I). Here it may be noted that some curves may result from constant motions of the sources of secretion, in cases where the growth lines are sinuous or where they converge strongly on the top and bottom of the whorl.

c) Motions of sources oscillatory. This type of motion appears to be rare in Mollusks, with the oscillations slow and of feeble amplitude (Pl. I, fig. 1: J) ex.: the radial sinuous bands of *Tricolia pullus* var. *lineata* Mtg.

secretion of elements begins at or near the margin, but continues further inside the shell, as if the secreting sources' radial motion could not keep up with shell growth. In many other shells (ex. *Pyramidella maculosa* Lam.) some pattern elements are secreted on the margin, others inside the shell aperture. In all these cases however, as opposed to the Cypraeidae, the secretion takes place along more or less broad bands or sets of lines that move radially with the growth of the shell, and not (with the partial exception of the yellow inner layer of *Telina radiata*) from the whole surface of the mantle.

<sup>7</sup> As indicated later, concentric patterns are rather rare. COMFORT (1964) appears to believe that such patterns would be dangerous to the animal displaying them. It may simply be that for such a variable phenomenon as colour secretion to take place exactly at the same time around the whole extent of the aperture would demand a degree of coordination on the part of secretion cells and all other factors leading to that secretion that might be impossible to obtain- unless a more fundamental phenomenon such as growth stoppage or sculpture were to directly influence the pigment cells at the mantle edge.

## 2. Secretion intermittent

In the case of intermittent secretion of oblique lines and bands, the individual fragments or spots produced most often seem to lose their obliquity and tend to be secreted as radially oriented fragments (in other words, instead of oblique rows of parallelograms one will tend to have *en échelon* rows of rectangles (Pl. I, fig. 2 a, instead of fig. 3). It is evident that in these cases intermittent secretion in oblique lines is associated with intermittent motions of secretory sources, the motion or shift taking place not as might perhaps be expected during secretion but between phases of secretion.

Finally, it might be said that the motions of sources of secretion need not necessarily be only sideways, but can be outwards and inwards within the shell aperture (P. I, fig. 4, spot secreted from A to B).

### *C. Extension or shrinkage of sources of secretion*

This can evidently take place sideways, or outside-inside like the motions, and especially may take place both on a macroscopic (for ex. to produce ovoid blotches as in *Natica millepunctata* Lam.) and a microscopic level (for the production of the minute projections from the bands of *Septaria janelli* Rcl.). It appears clear that many factors may be involved in these changes in width of secreting areas: the sources themselves may actually widen or shrink, different quantities of pigment might be secreted and hence perhaps spread differentially, the mantle may press harder or less so on the secretory areas, capillarity may become effective at times, etc.<sup>8</sup>.

### *D. Sources of secretion in contact with each other*

#### 1. Divergence and convergence of sources of secretion

These two terms are employed here only when the resulting elements diverge from and converge to a point (Pl. I, fig. 5, A and B). These two phenomena often occur together, as in the production of all zigzags and non-radial curves (Pl. I, fig. 7), but some shells show a high degree of dominance of one over the other (in

<sup>8</sup> A particular form of shrinkage-expansion is involved in the production of light spots in an otherwise dark shell (e. g. in *Anachis avara* Say): The usual shape of these spots, irregularly ovoid, appears to represent the one requiring the least amount of shape organisation on the part of the secretory sources: colour secretion fails along a gradually increasing region of the «secretion zone», then this «arid» region shrinks again, equally gradually, until secretion is restored throughout.

certain specimens of *Lioconcha castrensis* Lam. almost only divergent features (V's, etc.) are seen (Pl. I, fig. 6, 9), while in the «tent pattern» of *Oliva porphyria* L. convergences clearly dominate (Pl. VI, fig. 10; Pl. XI, fig. 9). A peculiar type of convergence is involved when two convex lines meet to form a lobe facing the aperture (Pl. I, fig. 5 E). The remarkable thing about such patterns is that they occur so often (for ex. in *Neritina meleagris* Lam. and *N. piratica* Rus.); for one would indeed expect two converging sources of secretion that appeared at different times during shell growth (Pl. I, fig. 5 F, a and b) and that after their inceptions often moved at different speeds, to be still moving at different rates when they met, and thus produce an angulation (Pl. I, fig. 5 F). Instead of this it appears clear that when they reach maximum (theoretically infinite) speed, they both do so at the same time, without, on the way, either source having had to abruptly modify this rate. The factor responsible for such a phenomenon is not directly discernible, but may be some kind of «resistance» in the area between the two sources that would gradually and evenly decrease or disappear, or conversely some «attracting factor» that would act in direct proportion to the closeness of the sources to each other.

## 2. Branching off and «inflowing»

These terms are used here to denote secretion phenomena and patterns wherein the elements diverge from and converge to preexisting elements that continue to be secreted without alteration in their course (Pl. I, fig. 5, lines C branching off from ab, lines D flowing into cb). While branching off is very common among Molluscan pattern phenomena (in most tent patterns for ex. Pl. VI, fig. 10), inflow is decidedly unfrequent (ex. in *Marginella lineata* Mühl.: Pl. X, fig. 8, *Sunetta scripta* L.). It is evident that when two sources of secretion moving in opposite directions meet, they most often both die out (for all zigzags, curves, almost all tent patterns, etc.); less frequently, both (in some way) appear to stay on each on its own course (see p. 11), and even more rarely does only one continue to do so.

## 3. 3-way junctions

These are formed when two sources of secretion meet, and after the junction there remains only one source, with a motion, if any, unlike that of either of the original sources. Junctions thus produced are not rare in hexagonal networks, see p. 31, Pl. VI, fig. 23.

## 4. Crossing of sources of secretion

### a) Crossing patterns on shell involving only oblique lines

Here we have two sources of secretion, both of very limited extent, that move toward each other, and then after the junction persist (or appear to do so), each apparently maintaining its own motion (Pl. I, fig. 11, lines AA and BB cross at D).

Spots which might be termed «*junction spots*», tend to form where the lines meet<sup>9</sup>: they are usually more or less rectangular in shape (Pl. I, fig. 11, D). They could be thought to be a pure effect of the junction (perhaps the result of capillarity or some similar process), but for the fact that often there is no direct relationship between size of spots and thickness of lines, and often indeed «*junction spots*» may occur in the absence of junctions (Pl. VI, fig. 11).

aa) Apparent crossing of lines may be seen in such shells as *Oliva porphyria* L. but on closer inspection it is evident that one of the two lines is secreted deep within the shell; the two sources of secretion thus passed one over the other, and never even met.

ab) In *Strombus vittatus* L. and related species, the pattern consist of closely spaced, highly unstable<sup>10</sup> transverse zigzags (Pl. I, figs. 7, 10, 12 and 13). Often more or less radial lines, which might be termed «*connective*» lines, appear between the zigzags, commonly but not always linking opposite points of successive zigzags (Pl. I, figs. 10, 13). It is possible that this «*point effect*» is related to the «*nearness effect*» mentioned later, wherein a source of secretion would not be shut off entirely between elements that are secreted in very close succession. The connective lines and zigzags here usually form hexagons and three-way junctions, but also sometimes rhombs with four-way crossing type junctions (Pl. I, fig. 13).

ac) In the same shells parallel but alternating zigzags may be joined at their tips, forming rhombs and crossing junctions (Pl. I, fig. 10, AB and CD). Of course in neither ab) nor ac) is any real crossing of sources of secretion involved, since the lines leaving the junctions do not belong to the same pattern features as those that converged to them (Pl. I, fig. 10: lines converging in x belong to zigzag CD, lines diverging from x to zigzag AB).

ad) Another situation obtains in portions of the last whorl of the Strombidae above mentioned (*S. vittatus* L., *S. canarium* L., *S. succinctus* L., etc.), as well as in number of Littorinidae (specimens of *L. fasciata* Gray, *L. zigzag* Gm., *L. melea-gris* Pot. and Mich., some Neritidae etc.). Here are found two sets of lines of opposite obliquity, neither one of which entirely dominates the colour pattern, but each one often being partially dominant over certain regions of the shell

<sup>9</sup> Sometimes we do not have junction spots. In *Piperita pupa* L. the lines involved are so thick relative to the network they produce that the cells are partly filled with pigment, and as a result of this the spot loci are all entirely submerged within extensive areas of black colouration. In *Tapes litteratus* L. we have junctions of contacting zigzags with spots poorly developed or absent altogether. This is not here the result of excessive secretion, but perhaps is related in some way to the strongly developed concentric ribbing of this species.

<sup>10</sup> How highly unstable, may be seen in Pl. I, fig. 12, and Pl. VI, fig. 11. In fig. 12 the central zigzag's angulations are turned both ways at once, evidently under the effect of opposite influences acting in a radial direction (the zigzags have a transverse orientation). Where the opposite tendencies act not radially but obliquely along the directions of the zigzag's limbs, these are prolonged until they meet the succeeding zigzags, and usually even much further. (Pl. VI, fig. 11).

surface <sup>11</sup> (Pl. I, fig. 11). There can be little doubt, it appears, that in junctions of such systems, sources of secretion do somehow cross each other's path <sup>12</sup>. It is a truly remarkable phenomenon of nature that two sources or waves of secretions can, like ghosts, race undismayed through each other, preserving unaltered their original characteristics!

ae) In a number of cases the lines of one of the two sets are thicker than those of the opposite set. This is often observed in *Littorina* Gm. *zigzag*, where the junction spots may be composed essentially of portions of the thicker lines. In *Littorina fasciata* Gray, these portions are often widely distant from each other, and may even be secreted on only one side of the thinner lines, just as in the junction figures mentioned below (p. 26). In *Littorina zebra* Donovan, on the other hand the thick lines are not segmented, but the portions of the thinner lines on the farther side of the junctions have shifted their positions relative to those on the near side (Pl. II, fig. 2), like in the bands of *Conus generalis* L. described below. The cases referred to in this paragraph represent a transition between these mentioned in the preceding and some of those to be described in the next paragraphs.

b) Crossing patterns on the shell not involving only oblique lines

In the following crossings, one of the two sources of secretion will usually be more or less static, and/or most often the elements secreted by each source will be different (in width, colour, etc.). In none of these crossings are junction spots found. The most noticeable phenomena here are the shifts of the portions of elements on the further sides of the junctions and the influence of one element over the other at the junction (Pl. II, fig. 7).

In these crossings, elements not produced by motions of secretory sources (i. e. radial and concentric elements) tend to be more stable than those that are thus produced.

The crossings mentioned here will involve the following elements and orientations:

Elements: *Lines and homogeneous bands*

Orientations: ba) concentric and radial

bb) transverse and radial

bc) transverse and oblique

Elements: *Homogeneous bands or lines, and alternating-colour bands*

Orientations: bd) Line or homogeneous band transverse to oblique,

alt. c. band radial

<sup>11</sup> Often these sets of oblique lines may make their appearance as emphasized and prolonged limbs of zigzags, or through stressing the oblique directions in a hexagonal network.

<sup>12</sup> Unless one can consider both sources as «shut out» during secretion of the junction spot, which in view of the shape, and secretion itself of the spot does not seem likely. Other possibilities such as a 180° race of the sources around the junction spots does not appear any more convincing!

ba) When concentric and radial elements meet, there is no shifting of the portions of elements on the far side of the junction (except in the case of some radial elements, where such shifting is related no doubt to the growth breaks and not to the concentric elements, as in *Neritina communis* Quoy, *Busycon contrarium* Conr.). If the elements are of different tints or shades (for ex.: one element colourless, the other dark), the junction will often be of intermediate shade, but may also have the shade of either component (Pl. II, fig. 1). All these possibilities are realized in *Busycon contrarium* Conr.

bb) In the case of *Conus lucidus*<sup>13</sup> Wood and *Bullina lineata* Gray, «lobes» and transverse wavy lines respectively are crossed by radial lines, and the segments of these transverse elements on each side of the junction tend to be discontinuous.

The same applies in the case of *Conus generalis* L., where the radial element is a thick band, but we have here often in addition a shift of the segment of the transverse line within the band in relation to the segment on each side of it (Pl. II, fig. 7). The segments within the band tend also to lose their waviness and to become strictly concentric in orientation; they also tend to be lighter and often additional segments may appear here. Where the colour secretion in the band is poorly developed, however, the transverse lines may cross it unchanged; even more so where the band is interrupted, but in this case a fragment of the band will usually appear at least on the distal side of the lines, very much as in the junction figures mentioned below (p. 26). In *Imbricaria conica* Desh. the situation is reversed from that of *Conus generalis* L., for here it is the transverse element which is a band, the radial a line. The transverse element is here also usually reduced to segments with discontinuous positions, but in the present case the bands also produce effects on the lines, or have an influence on them<sup>14</sup>: for not only may they penetrate partly or wholly through the lines, but when the band segments alternate on each side of a line, this one, curving around the end of each portion, may become slightly sinuous (Pl. II, fig. 3; Pl. X, fig. 1).

bc) In *Tricolia tessellata* Phil. we have a pattern not unlike that of *Conus lucidus* Wood, only here the stable component is not quite radial, but slightly oblique: in addition to transverse lines, there are also episodic transverse bands

<sup>13</sup> In *Conus lucidus*, transverse lobes, generally speaking, appear between the radial lines, several lobes being often connected transversally to form lobate lines. It is however uncertain as to whether lobate lines constitute really the «original» transverse pattern; for the fact that the lobe apices generally fall out at about the level of the inspace center, and that when one or more radial lines are interrupted, the lobes extend distally until secretion of the radial elements is resumed (Pl. II, fig. 4; Pl. X, fig. 2, center of specimen) in which case the renascent lines emerge from the lobe apices, make it evident that the aspect of the transverse component is strongly influenced by the presence of the radial one: what the appearance of the first would be in the total absence of the second is not too clear.

<sup>14</sup> In all these crossings, where an element has an «influence» on another (as for ex. the influence of the radial bands of *Conus generalis* L. on the transverse lines which cross them), it is evidently the secreting of the element, not the element secreted, that produces the influence.



as in *Imbricaria conica* Desh., which likewise produce slight bends in the lines. As the transverse lines of *T. tessellata* are rather regularly distributed, they may form with the oblique lines various types of networks, often with rectangular cells (Pl. II, fig. 5).

bd) The influence of elements on each other is especially noteworthy where transverse bands cross radial alternating-colour (alt. c., for short) bands. At the place of junction, even though the transverse band may not cross the alt. c. band, the portions of the latter with a coloration or shade similar to that of the former (the «like» portions) will be favoured over the alternate portions (the «unlike» portions), whether in their relative extent, and/or the intensity of their colouration: the unlike portions may also even adopt in part the colouration of the «like» portions (Pl. II, fig. 6)<sup>15</sup>. For ex., in *Gibbula ardens* v. Salis, there are transverse bands of both white and dark brown colouration: these influence and sometimes traverse alt. c. bands with equally white and brown portions: where the brown bands join the radial alt. c. ones, the brown portions of the latter become wider, and as dark as the transverse bands, while the white portions may also show a more or less vague brownish hue: the opposite happens in junctions with the white transverse bands.

Where the transverse bands actually cross or transect the radial alt. c. ones, i. e., where the junction areas will have the colour of the first, at least three alternative or conjugate processes will have acted on the alt. c. bands: (1) Expansion of the «like» portions until they reach the width of the transverse bands (2) A complete alteration of the colour of the unlike portions to a colour like that of the transverse bands, (3) Pigmentation similar to that of the transverse bands spreads more or less evenly all over the junction areas. The two first phenomena have been observed in *Gibbula ardens*, the last two in *Charonia variegata* Lam. (Pl. X, fig. 3).

Two species have been here studied where the transverse elements of patterns like that just mentioned are lines rather than bands: *Natica canrena* L. and *Monodonta articulata* Lam. (Pl. II, fig. 9; Pl. X, fig. 4). In the first species, transverse brown lines cross alt. c. radial bands with brown and whitish portions: the crossings take place through the brown portions, usually apparently at the rear ends thereof, and never, or almost never through the white portions<sup>16</sup>. In *Monodonta articulata* Lam., we have alt. c. bands of red and white rectangles crossed

<sup>15</sup> Where, as in *Turbo petholatus* L., the «like» portions stay small, they may multiply abundantly.

<sup>16</sup> Numbers of such crossings through the white portions of the alt. c. bands may indeed be observed in *Natica canrena*, but this almost always appears to be in regions where the bands are secreted well below the shell surface, and the level at which the transverse lines occur. — The junctions of the transverse lines and dark portions of the alt. c. band form a pattern (= junction figures, see below p. 26) similar to that of transverse lines with spots from a row of such, as in *Conus striatus* L., etc. This is presumably an indication of the close relationship between at least certain types of spot rows and alt. c. bands.

by black transverse lines: here the crossings almost always take place at the posterior boundary of the red rectangles, sometimes through the rectangles, but never, in the specimens at hand, through the white rectangles (Pl. II, fig. 9).

*E. Sundry colour secretion phenomena: influence, secretion gradient, etc.*

In some cases, the influence of one element on the other is much more distinct than the element itself that produces it: in fact in numbers of cases the presence of an element can only be guessed at by the influence it exerts on some phase of the pattern: in *Conus mediterraneus* Brug., the white blotches of the radial alt. c. lines may become much more important and/or numerous along certain transverse zones. In *Conus arenatus* Brug. the spots of an otherwise relatively homogeneously spotted field will, along certain radial directions grow bigger, darker, and/or more numerous: the intermediary spaces may also grow slightly darker (Pl. II, fig. 10). In both these cases the pattern component or element producing these changes is hardly or not at all to be seen, and may be referred to as «latent». Such a component in terms of secretion might simply mean that it manifests itself only where pigment (whether coloured or white-opaque) already appears, and not by covering uniformly the whole surface of the shell.

A phenomenon allied to the preceding is that which might be termed «secretion gradient», where the change in pigment secretion is gradual rather than abrupt. Thus at the base of many cones (*C. vexillum* Gm., *C. virgo* L., etc.) there is a tendency for the colour to get gradually darker. In *Nautilus pompilius* L., this gradient is to all evidence expressed in the same way as was the «latent» component mentioned above: the greater amount of pigment available at the center of the whorl produces bands wider and more numerous (though not appreciably darker) than the gradually weakening secretion on the whorl sides. The bands in the latter areas also often flex distally as if the secretion there were not only less prolonged, but also slower to appear: this flexion, incidentally also appears in many cases when a non-radial line crosses a radial zone devoid of pigment, as in the light bands of *Voluta scapha* Lam.

We might have a phenomenon just opposite to that observed in *Nautilus pompilius*: here colour secretion would be about equal over the whole shell margin (as deduced from the generally even darkness of the whorl over its width) but the trajectory of the lines would require strong differential colour secretion if the lines were to maintain their thickness and number. In *Voluta undulata* Lam. the sinuous curves are much closer on the sides of the undulations than at the extremities (Pl. II, fig. 8). If these lines were of even thickness and equally numerous throughout, strongly pigmented radial bands corresponding to the curve sides would be produced, evidently requiring a greater output of pigment in the corresponding marginal region than for the production of the lighter alternate bands. Since this does not obtain, the lines on the curve extremities will be thicker

and/or more numerous<sup>17</sup>. In the case at hand they will tend to be much thicker on the distal ends and more numerous on the proximal ends of the curves. The phenomenon above described, which might be termed «compensation phenomenon» (the thickness of the bands in one place compensating for their greater number elsewhere) is also found on the whorl sides, where secretion is slower and the growth lines converge. There concentric lines and bands will often become thinner, or lighter (*Busycon contrarium* Conr.), while transverse lines may also show other compensatory tendencies (fewer lines, etc. in *Rissoa lineolata* Mich.)<sup>18</sup>.

Another important «effect» or «influence» only remotely related to crossings concerns lines secreted in close proximity (whether in the radial or concentric direction): the empty spaces between such lines will tend to be filled with a greater or lesser amount of colouring matter (Pl. II, fig. 11) as if the proximity of other sources of secretion or of a new phase of secretion prevented the secreting cells from being «shut off» entirely. This effect will be referred to here as the «nearness effect». It is presumably because of this effect that fine-meshed «reverse» networks (i. e., networks with a colourless frame and pigmented cells, see p. 34) were not found on any specimen: the only reverse networks observed, such as that of *Babylonia ambulacra* Sowb. had a frame as thick as entire cells of «normal» networks, like those of *Strombus vittatus* L.<sup>19</sup>. The «points effect» cited above as manifesting itself between the points of adjoining zigzags may be a variant of the nearness effect; and the fine threads that often bind together the retangles of a checkerboard pattern, or the closely-set dots of the crossed-oblique dotted pattern of *Tricolia pullus* L. may likewise result from this phenomenon.

Influence on elements of a pattern may be produced not only by other elements of the pattern or by phenomena of colour secretion, but by other features of the shell, such as sculpture (see below, p. 44) and growth breaks. The influence of the latter may show itself in at least three ways: (1) By movements of elements along the line of the break, producing, for ex., discontinuities in the radial bands of certain *Polymita picta* Born (Pl. II, fig. 12a), (2) By partial or total interruption of colour secretion on the far side (and sometimes on the near side as well) of the break, the colour intensity increasing thence gradually to its former level (12b). (3) By a change in orientation of lobate or irregular transverse lines, or transverse

<sup>17</sup> The greater number of lines there might theoretically result from: — (1) Appearance of intercalary lines, (2) Bifurcation of lines, (3) Overlap of interrupted lines. Only (1) and (3) were found to occur in this case.

<sup>18</sup> NEUMANN (1959) has noted the reduced number of lines on the whorl sides of certain *Theodoxus*, as also the concentric orientation of otherwise transverse elements immediately after growth breaks. It seems likely that other effects mentioned in this work will have been observed by authors of monographs on various species of Mollusks, but such observations have not come to the attention of the author.

<sup>19</sup> This «rule» should probably apply only to frameworks that are actually pigmentless, and not to those formed by white opaque pigment, as in *Helix aspersa*, though in fact the network of that species is rather coarse too.

alignments of spots, to a specifically concentric orientation, with thereafter a gradual return to the original set. Such a phenomenon may be observed for the lobate lines in *Harpa major* Röd. or the transverse alignments of *Conus litteratus* L. (Pl. II, fig. 13).

#### IV. Geometric classification of possible patterns (produced from a line)

##### *A. Introduction*

There is, because of the variability in animal forms and the variety of environments, a tendency in any large systematic group for many or all of the potentialities of a given situation to be realized. Thus mammals and reptiles have both conquered land, sea and air; differential growth rates along the horn cores of the Bovidae will lead to the formation of straight horns, of horns curving forward, backward, spirally, helicoidally, etc.; the same applies to the shells of fossil cephalopods and Recent gasteropods. It might be of some interest to ascertain to what extent such tendency to multiformity obtains in the patterns on Recent Molluscan shells.

As is well known and indicated above (p. 7) most such patterns, and all those studied here, may be considered for most practical purposes as being secreted from a single line at the shell's aperture. Since an infinite number of patterns can theoretically be thus produced, to make an evaluation of actual pattern variability in the terms stated above will require at first grouping and classification of all these putative patterns; once this is done it should be feasible to establish which of these pattern types is actually represented in the mollusks and which not, and perhaps in some cases it might be possible to imagine reasons for the non-appearance of some types.

To make such a classification of patterns on a purely geometric basis is probably impossible, as there would be as many classifications as geometers and indeed probably many more. Such an attempt would moreover require a more objective point of view than a conchologist is likely to have: the present classification of patterns will thus admittedly be to some extent influenced by what the author has actually observed to occur on shells. So long, however, as the main possible types of patterns are included in the classification, its malacological «weighing» will, it is hoped, not unduly limit the validity of the comparison between theoretical and actual patterns. Many of these patterns are illustrated on Pl. III and Pl. IV, figs. 1–15.