Zeitschrift: Mitteilungen der Naturforschenden Gesellschaft in Bern
Herausgeber: Naturforschende Gesellschaft in Bern
Band: 25 (1968)

Artikel: Remarks on colour patterns and related features of the Molluscan shells
Autor: Oberling, J.J.
DOI: https://doi.org/10.5169/seals-319553

Nutzungsbedingungen
Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Mehr erfahren

Conditions d'utilisation
L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. En savoir plus

Terms of use
The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. Find out more

Download PDF: 06.01.2026

ETH-Bibliothek Zürich, E-Periodica, https://www.e-periodica.ch

J. J. Oberling

Remarks on colour patterns and related features of the Molluscan shells

Acknowledgments

Prof. Dr. W. Huber generously made available Museum funds for the publication of this article, made many helpful suggestions and is responsible for the photographs. Miss V. Gerber helped greatly in preparing the work for publication. The author expresses his warmest thanks to these persons for their help.

Table of contents

I. Introduction 4

II. Terminology 6

III. Presumed activities of sources of secretion 6
- A. Sources of secretion stationary 7
- B. Sources of secretion ambulatory 7
- C. Extension or shrinkage of sources of secretion 8
- D. Sources of secretion in contact with each other 8
- E. Sundry colour secretion phenomena: influence, secretion gradient, etc. 14

IV. Geometric classification of possible patterns 16
- A. Introduction 16
- B. Categories of pattern elements 17
  - 1. Linear elements 17
  - 2. Non-linear elements 18
- C. Arrangements and configurations of elements 20
  - 1. Arrangements of «small» elements 21
  - 2. Components 23
  - 3. Networks 27
  - 4. Sundry pattern types 36
  - 5. Periodicity 37

V. Ontogenetic development of colour patterns 38
- A. Introduction 38
- B. Examples of pattern ontogeny 40

VI. Relation between colouring and sculpture 43

VII. Interrelationships between pattern elements 48

Abstract — Zusammenfassung 50

I. Introduction

While looking over the collections of the Museum of Natural History of Berne, the author could not help being struck by the remarkable variety and often extreme complexity of the colour patterns of the Molluscan shells. It might even appear at first sight, that there is hardly any geometric or irregular design which is not represented on some specimen or other from these collections: squares, polygons, networks, checkerboards, labyrinths, bright, sharply delineated bands, zigzags, vague blotches, the variety appears endless and is certainly unsurpassed in the animal kingdom[1] – this in spite of the fact that most molluscan colour patterns are produced, so to say, from a single line and not from a complex surface, as are those of most other animals.

Equally remarkable is the variety of relationship between colour patterns and the other features of the shell, notably the sculpture: one need only bring to mind on one hand certain Harp shells wherein the entire colour arrangement seems to be controlled to the minutest detail by the ribs and varices, and on the other hand Volutes on whose shells complex reticulations may be seen to continue unchanged almost to the very tips of the spines. It is this extreme variety in the colouration and in all these relationships which makes any classification of these phenomena, any setting up of general «laws» such a hazardous proposition. Almost as soon as such a principle is established, exceptions are discovered and often become in the end so numerous that the principle is seen to have become a mere matter of statistics, a mere probability. Such is the case for Wrigley's dictum that «light elements of colouration in gastropods occur on or represent the raised spiral bands and the knobs and spines found upon them, while the dark colourings are confined to the depressions between the salient parts of the sculpture» (WRIGLEY, 1947, p. 206). This law is certainly very often true, but exceptions to it are far from rare! In many Muricidae (*M. radix* Lam., *M. torrefactus* Sowb., etc.), Buccinidae (*B. lineatum* Lam., *B. undosum* L., etc.), Mitridae (*M. filosa* Lam., etc.), Rissoidae (*Alvania lineata* Risso, *A. Montagui* var., etc.) Planaxidae (*P. lineatus* Costa, etc.), and no doubt also in other families spiral ribs, whether they be wide or narrow, are darker than interspaces. As will be again indicated later, ribs are often associated with bands of alternately lighter and darker colouration, with usually not the slightest indication that the light elements were ever associated with tubercles.

[1] There is, however, nowhere on Molluscan shells such a complex eye within eye structure as is to be found on peacocks (birds) and peacocks (butterflies). In *Cypraea argus* L. we have merely a circle within a circle; in *Cypraea zebra* L. a dark blotch within a white one; in the more common shells, where the colour patterns are secreted at the margins, even such simple «eyes» are lacking. In various Neritinas, one gets black rims around light spots, and even rather astonishing eye-lash like features (as for ex. in *Neritina pulchella* Recl.), but there is seemingly nowhere a complete closure of the rim around the «eye».

In such a species as *Alvania montagui* Payr. s.s., one finds light-coloured ribs that become almost black on the final varix, that is, on a prominence, and near the base of the whorls a number of ribs with alternate dark and light segments. As for tubercles and spines, it will suffice to mention that in the case of *Clanculus pharaonis* L. they are alternately black and white on the main ribs; and that the spines of *Murex radix* Gmel. show beautiful funeral-black tints! It serves no purpose therefore to assert as WRIGLEY does, that exceptions to his rule are not really exceptions (p. 27). They are and it is the «rule» that is no rule but simply a statement of a frequent occurence [2].

The present work is meant to be a generalized preliminary study of colour patterns and related features of the shell (the author hopes to be able to follow up on this study with a more comprehensive one at a later date), such as those already presented by WRIGLEY (1947) and in a more popular vein by COMFORT (1964)[3], but undertaken here in a somewhat more systematic manner.

There are a number of possible bases on which such a work could be produced; these would include:

A. A study of the presumed (and whenever possible, real) activities of the sources of secretion in the production of the different patterns, etc.

B. A study of the patterns themselves, so as to enable one to try to group those that are similar, etc.

C. A study of the theoretical possibilities of pattern production (from a simple line in most mollusks), classification of these putative patterns in order to determine which of these are actually present on the shells and which not, and whenever possible, determination of the reasons for the failure of certain patterns to appear, etc.

D. Analysis of the ontogenetic (and when possible phylogenetic) development of patterns on the shell.

E. A study of the genetical, biochemical and ecological basis for pattern formation and its application to the explaining of all the different existent patterns.

The last base is of course the only one on which a truly scientific study of patterns can be undertaken. But until this is achieved, attempted classifications on the 4 other bases, though they will necessarily be of a superficial character, may not be absolutely useless, for they will call attention to similar phenomena in different groups and may even in the end furnish a preliminary basis for the really decisive genetical study.

[2] This paragraph is not meant to be a condemnation of Wrigley or his works! That author had on his own account very little material at his disposal, and was compelled to base all his conclusions on pictures from old and threadbare conchological manuals. With such a basis as this, his findings will appear almost miraculous!

[3] A short time before publication of this work, the author's attention was called to an article by NEUMANN (1959) on *Theodoxus fluviatilis* L. The findings of that author that especially concern the topics here treated will be mentioned in the appropriate chapters.

II. Terminology

In the present work, which though it necessarily emphasizes the Gastropoda [4], 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 [5]

(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 [6] the external coloration of all Mollusks is produced from the mantle edge, and indeed for most purposes may be considered as

[4] 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.

[5] «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 prejudge 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).

[6] 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 [7], 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 *Tellina radiata*) from the whole surface of the mantle.

[7] 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 becomme effective at times, etc.[8].

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

[8] 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 decidely 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 [9]: 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 [10] 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. meleagris* 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

[9] 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.

[10] 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 [11] (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 [12]. 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* Donov. 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

[11] 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.

[12] 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* [13] *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 loose their wavyness 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 [14]: 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

[13] 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.

[14] 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)[15]. 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[16]. In *Monodonta articulata* Lam., we have alt. c. bands of red and white rectangles crossed

[15] Where, as in *Turbo petholatus* L., the «like» portions stay small, they may multiply abundantly.

[16] 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 extremeties (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 [17]. 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.) [18].

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. [19]. 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

[17] 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.

[18] 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.

[19] 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-apparition 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.

B. Categories of pattern elements [20]

1. Linear elements

Straight radial lines are extremely common on molluscan shells, as may be perceived at a glance on almost any garden snail: straight lines with other orientations are on the contrary quite rare: (a) truly concentric straight lines and bands do not appear possible, or at least could not be found in the specimens at hand, unless associated with other periodic phenomena or structures (in all cases studied, with growth breaks of one type or another – ex: in *Busycon contrarium* Conr., *Arianta arbustorum* L.); (b) apart from these, straight transverse lines have been observed in some specimens of *Rissoa lineolata* Mich., and straight (more or less) oblique lines in *Tricolia tessellata* Phil. and *Neritina glabrata* Sowb.

Interrupted straight lines, like the non-interrupted ones, are likewise almost always radial.

Non-straight lines, as opposite straight ones, are almost never radial: many have axes directed more or less concentrically, or to use Cox's terminology (Cox, 1955) their axes are transversely oriented. Of all these lines, the zigzags, the irregular lines with oriented axes, and the convergent lines are the most common.

Convergent lines may appear alone as chevrons (as in *Neritina communis* Quoy), in association with branching lines in «tented» networks (as in *Oliva porphyria* L.), or with divergent lines in zigzags, etc.

Divergent lines, apart from the last occurence, are not too common, but may be found alone or in association with branching lines, for ex. in varieties of *Lioconcha castrensis* Lam.

Zigzags are extremely common in the Gasteropoda and in the Veneridae among Pelecypoda. They may be of the simple type (*Voluta undulata* Lam.) or of the complex type, with secondary angulations superimposed on the primary (*Voluta scapha* Gm.). On the other hand the zigzags may be stable, with any zigzag very much like the other, as in *Voluta undulata* Lam., or unstable, that is highly variable, tending to divide into secondary zigzags, or to become connected with the neighbouring ones, as in *Strombus vittatus* L. (Pl. I, fig. 10). Zigzags may also be fused into various kinds of networks (Pl. I, fig. 10; Pl. XI, figs. 5, 9).

There are all kinds of intergradations between the various zigzags, and sinuous lines: such elements, which are not specifically either the one or the other, might

[20] Pattern elements and patterns may be «normal» (with the figures darker than the ground), or «reverse» (with the figures lighter, as for ex. the zigzags of *Columbella fulgurans* Lam., the irregular «tented» pattern of *Mitra fissurata* Lam., etc., see also p. 34). Such reverse figures may be light because of an absence of pigment (true reverse figures, probably represented in *Columbella fulgurans*) or the presence of a light pigment (pseudo-reverse figures, as in *Helix aspersa* Müll.). As the presence or absence of pigment in such cases is often hard to determine on a mere examination of the shell, reverse figures or patterns will not be further distinguished. Some shells, finally, for ex. specimens of *Pecten glaber* L., show both dark and light figures on a greyish ground!

be termed irregular lines, and are well represented by the remarkable array of parallel lines of *Neritina reclivata* Say.

Lobes, like simple curves (Pl. III, fig. 4 d) and chevrons usually span only a small portion of a whorl's width: they are found frequently in the Neritidae (*Neritina meleagris* Lam., etc.) and Conidae (*C. omaria,* etc.).

Lobate lines made of contiguous lobes of identical orientations (Pl. III, fig. 5 c) will in reason of their complexity be rarer than single lobes, but may be found in *Tricolia tessellata* Phil. (convexity towards aperture) and various *Harpa* (convexity usually towards the apex).

Ogives [21] (or approximations thereof) are found in many Conidae, where they are generally known as «tents», from their supposed resemblance to these military or nomadic objects (as in *C. omaria* Brug.).

Crenations are rare, as they involve two components in rather complex relationship to each other. Trapezoidal crenations of a sort appear in some peculiar networks: In the young *Bulla striata* Brug. they are produced, to all evidence, when connective lines join together similar portions of contiguous alt. c. bands (the portions in question have the shape of thick transverse lines; Pl. VI, fig. 20). Rectangular crenations as such have not been observed and are extremely unlikely to occur, for radial elements (= sides of crenations) would not normally cease being secreted on meeting transverse elements («tops» and «bottoms» of crenations), and especially not twice in a row.

Lobate crenations on the other hand, though not of a very regular type, have been found in some species where a lobed pattern is associated with a pattern of transverse lines, for ex. in *Neritina meleagris* Lam. and *Conus textile* L. (Pl. V, fig. 8).

2. Non-linear elements

These may appear, in increasing order of magnitude as dots, spots, blotches and areas. The limits between all these are arbitrary: blotches are usually considered to be rather big and irregular spots.

Spots may be derived, among other things, from: (1) Bands, either when these break up as in *Rissoa guerini* Recl. (Pl. I, fig. 2 a), or when they are transected by sharp sculpture, as in *Littorina tessellata* Phil.; (2) Homogeneously coloured surfaces, when these become divided as in *Mitra mitra* L. or *M. pontificalis* Lam. (Pl. VIII, fig. 2); (3) Bigger spots which also divide, as likewise in *Mitra mitra* L.

Spots may theoretically have all possible shapes, even that of stars or crosses (Pl. IV, fig. 1 n, o), but actually are either more or less irregular, or may show various approximations to simple geometric figures, essentially ovoids and polygons. The latter, or regular spots, will be considered first:

[21] The term «ogive» is here used for the dark line surrounding the distal part of an ogival-to nail-shaped light spot or ocellus.

Circles, ellipses, ovals and ovoids are more or less vaguely approximated (esp. in the light spots of ocellated patterns such as those of *Nitidella ocellata*), but their exact reproduction except by a «lusus naturae» would not be expected, as this would require a remarkable feat of precisely accelerated expansion and shrinkage of secretory zones, especially as one must take into account here the continuous radial shell secretion with which all these processes would have to be coordinated.

Rectangles, more or less approximated, are perhaps the most common type of regular spot shapes to be found in molluscan shells, perhaps because they generally include both transverse and radial sides, and these are the most frequent orientations in shell patterns. Squares are more regular rectangles for which the product: (period of secretion) x (speed of shell growth) would have to correspond exactly to the width of the element: as may be expected from this, they will be relatively scarce.

Rectangles are frequently found in lines of spots (Pl. IV, fig. 16), alt. c. bands (Pl. II, fig. 9), on ribs (the rib sides forming the sides of the rectangles – Pl. VII, fig. 20), in networks, as junction spots (Pl. VII, fig. 22), in checkerboards (Pl. VII, fig. 22 top), and in general, as fragments of bands which have dissociated (Pl. I, fig. 2 a), or are cut off by varices or ribs.

Triangles, trapezes, rhombs and parallelograms may be associated with rectangles in alignments of spots as in *Mitra mitra* (Pl. IV, fig. 16): they might in such cases be considered as «incomplete» or poorly developed rectangles. Light rhombs and parallelograms are common in networks, as indicated below. Triangles may appear as junction spots in some networks (as in some *Conus marmoreus* L.), are often associated with diverging lines (for ex. in specimens of *Lioconcha castrensis* Lam., and others species of that genus), or may appear alone scattered on the shell surface (*Neritina piperita* Chemn., *Lioconcha tigrina* Lam.). In the last three types of occurences, the triangles have a side facing distally. In some other patterns, the triangles «fill in» the space between two converging lines, and have a side facing proximally (species of *Placostylus,* such as *P. hargravesi* Cox, *P. sanchristobalensis* Cox). Finally triangles or close approximations thereof may be found in some checkerboard networks (Pl. VII, fig. 18).

Trapezoids may, among other occurences, show up as fractions of radial bands, when such bands widen rapidly, as in a number of pelecypods (for ex. in *Pitar inflata* Sowb.).

Rather elongate hexagons may be found in the network patterns of some *Babylonia,* especially *B. ambulacra* Sowb. and the light or colourless varieties are also limited essentially to networks, as are octogons, and even pentagons (Pl. I, fig. 13).

That such polygons are not found as isolated units like triangles and rectangles may imply a lack of organizing complexity in the secretion of unit areas.

Spots or dots may be irregular in different ways:

(1) Their general shape may be devoid of any symmetry, being vaguely tear-shaped, ovoid, etc., (2) They may show marked macroscopic projections of various sorts (Pl. IV, fig. 18): spots or blotches of this type, called here «junction figures» (p. 26) are usually found in places where two or three periodically appearing components are associated (as in *Conus striatus* L., see p. 26); (3) the outlines of the dots (and that of other patterns, for that matter)[22] may not be sharp and distinct but more or less blurred (Pl. IV, fig. 17 a–d). This blurring may theoretically, and apparently also practically, result from at least five causes or various combinations thereof: (a) the colouring may be less dense or dark at the periphery of the dot (fig. 17 b); (b) the thickness of the colour secretion (i. e., of the dot) may be less great at or near the periphery (fig. 17 a) or c) the secretion may there be further removed from the shell surface (fig. 17 c); (d) the shell substance outside or above the dot may be more opaque at the periphery than above the center (fig. 17 d); (e) the dot may have microscopic projections which may contribute to the blurring of the outlines, if viewed without optical instruments. These different factors will of course certainly never appear in as pure a form as in the illustrations, but may be associated in various ways. Factor (d) has not yet been detected with certainty, but all others may appear in the dots and blotches of *Natica millepunctata* Lam., *Tricolia pullus* L., various Olives, etc.

C. Arrangements and configurations of elements

In a consideration of the various types of possible distributions and arrangements of pattern elements on a whorl or valve, the character of an element (linear or non-linear) is not as important as its span: for ex., the possible and actual distributions of linear elements like lobes will be much more akin to that of non-linear elements like spots (Pl. IV, fig. 19 a and b) than to lobate lines (fig. 19 c). The arrangements of elements with a limited span («small elements») will be considered first separately. «Big» elements are either parallel, touching or crossing. Parallel elements will be considered especially in the chapter on «periodicity»; crossing elements, when the crossings are not frequent enough to produce networks, in the chapter on «components». «Big» elements, generally of a kind, that cross repeatedly or are in contact produce networks and will be considered under that heading, together with the «small» elements that produce similar patterns. In networks, indeed, the character of the element is again of utmost importance: for ex., isolated lobes and lobed lines might theoretically produce the same type of scaly pattern (Pl. VII, fig. 13); moreover networks are best classified according to whether all, half or none of the cells are coloured («reverse», «checkerboard» and «normal» networks respectively), or in fact whether the geometric

[22] For ex. the diverging angles of some *Lioconcha castrensis* and many Olives, which have sharp apices, but are continued only as vague shadows (Pl. I, fig. 9).

basis of the pattern is linear (normal networks) or non-linear (the other networks). In the chapter on networks thus, the character of the elements rather than their span will be emphasized.

1. Arrangements of «small» elements (that cover only a portion of a whorl's width)

Non-linear and linear elements of limited extent (dashes, short lines, angulations, etc.) may theoretically be arranged in practically an infinitude of ways (Pl. IV, figs. 2–10): only a extremely limited portion of all these possible arrangements was actually found by the author.

Truly irregular arrangements of elements, whether of the homogeneous or clustered type (Pl. IV, figs. 2, 3) have not been observed on any shell with marginal secretion: the existence of such patterns seems to be limited to the Cypraeidae, with *C. pantherina* Sol., etc. showing the (more or less!) homogeneous, and *C. erosa* L. the clustered type. In margin-secreted shells there is as indicated later (p. 23) a tendency for elements to occur in sets either iterative or periodic, and this type of regularity is most often only modified, not eliminated, by the differential growth and fusion of elements in some patterns, such as the «tent» pattern within the bands of *Conus textile* L.

Unidirectional patterns (Pl. IV, fig. 6) are not at all common [23], for if they are radial, as for ex. in *Mitra mitra* L. and *Voluta indica* Gm., there is a tendency for the spots in all these radial lines to be secreted at about the same time: and we will thus have transverse alignments as well; on the other hand if the alignments are primarily transverse, as appears to be the case for *Conus chaldeus* Röd. (where the elements are to all evidence segments of transverse bands), the segmentation itself will result from the lack of colour secretion on certain portions of the mantle margin, and thus these spots will be also radially aligned (Pl. V, fig. 3). There are many species such as *Conus litteratus* L. where the two tendencies are so well balanced that it is hard to be sure at a glance which tendency is the primary one.

If the arrangements, radial and transverse, are relatively regular, the elements will automatically also be arranged in oblique rows (Pl. V, fig. 2, rows x and x'). This does not appear, however, to be the origin of the oblique arrangement of spots in most patterns studied (for ex. that of *Natica millepunctata* Lam., *Tricolia pullus* L., etc.) In the first species, radial arrangements are often absent, even in the presence of oblique ones, and in the second there often appear authentic linear zigzags. In both it is evident that the oblique pattern (with an arrangement of dots in two directions of opposite – and often equal-obliquity) is the

[23] Not common, but by no means nonexistent! When the lines of dots are separated from each other by important structural or pattern features, the dots will tend not to correspond from one row to the next: such is the case for the rows of dots on either side of the subsutural groove in various *Terebra,* such as *T. subulata* Lam.

essential feature. This pattern may be termed «crossed-oblique». It may represent, as apparently do most rhombic regular networks, a kind of «conflict» of dominance between two oblique directions: the rather irregular transverse arrangements in those patterns may reflect only an imperfect periodicity in spot production [24]. The radial (more or less) arrangements of spots that are often seen when such patterns are relatively regular probably derive directly from this regularity (Pl. V, fig. 1).

The arrangement of ocelli in the ocellate pattern of *Nitidella ocellata* Gm. is very similar to the arrangement of spots in *Tricolia pullus* L.

In all these patterns the spots will generally be much farther apart along the radial than along the three other directions.

Crossing lines or bands of small elements (Pl. IV, fig. 10) are rather rare among shell patterns. The best examples observed were in *Conus pulicarius* Brug. for dots and in tent cones (*C. omaria* Brug., *C. textile* L., etc.) for lobes.

Cases in which one element is within another, or is part of another, are numerous (Pl. IV, fig. 14 d), but do not show a great variety of types:

(1) Alternating colour (alt. c., for short) bands and lines (Pl. V, figs. 4–7, Pl. II, fig. 9, etc., etc.) are extremely common among gastropods, but are rare and not fully developed, it seems, in any pelecypod known to the author. Isolated portions of alt. c. bands may be considered in a way as elements within elements, if the fragments or portions of each colour are themselves deemed to be elements, and not simply different phases of one thing (the band). The diverse origins of these bands will be indicated (p. 40). There are all kinds of gradations between simple rows of dots and fully formed bands. The band itself is defined in different ways from the rest of the shell: both elements of the band may be darker than the rest of the whorl (*Liguus blainianus,* Pl. VIII, fig. 1); one may be darker, the other lighter (the most common occurence: *Gibbula ardens* v. Salis, *Phasianella australis* Gm., *Conus aulicus* L., etc.); one element may have a different shade, the other a different colour (*Monodonta articulata* Lam., etc. Pl. X, fig. 4). The boundary between band and rest of whorl may be emphasized if it corresponds to the limit of sculptural elements (to the rib sides in *Charonia tritonis* L. and *Clanculus pharaonis* L.); or if the light element is framed in dark lines (*Liguus blainianus* Poey, Pl. VIII, fig. 1).

The shape of the elements within the bands is also highly variable. In most cases we have more or less rectangular figures (*Gibbula ardens, Monodonta articulata, Liguus blainianus,* etc., Pl. VIII, fig. 1). In other cases the dark element may be lobe-shaped and surround or partly surround the light element (*Charonia variegata* Lam., some *Neritina oualanensis* Lesson, etc., Pl. V, fig. 16); in others the light element may appear as irregular zigzags set in the dark element composing most of the band (*Turbo petholatus,* etc.).

[24] Directly after growth breaks, these spots will usually be concentrically arranged, the ordinary, more irregular transverse arrangement being gradually resumed thereafter.

In alt. c. lines we have usually a dash and dot arrangement, with the dark element forming the dot (*Pisania pusio* L.), or more commonly the white one (*Conus mediterraneus* Brug.).

(2) Ring within ring arrangements are only to be observed in Cypraea such as *C. argus* L., not studied here; apart from that, in the normally secreted colour patterns no such feature could be detected, or nothing like the «eyes» in butterflies [25].

(3) Differential striping within bands, often evidently owing to sculpture «influence», has been observed in many cases (*Arca zebra* Swains., *Conus striatus* L., etc., see also p. 44).

(4) Inside bands may be found elements which are also distributed on the rest oft the shell surface. Such elements will have no real relation to the bands (ex.: the alternate colour lines of *Conus nussatella* within the brown transverse bands of that species). These elements within the areas of the bands may be set out, emphasized or otherwise affected (such in a way is the case, for ex., of the irregular network of swellings in *Helix aspersa* Müll, which is filled with white pigment inside the radial and transverse bands; or the blotched pattern in *Bulla striata* Brug. with strongly emphasized blotches within the radial bands).

(5) Finally in some Gastropoda, the minor pattern features distributed within the bands will be more directly related to the major units. For ex., in *Conus adamsonii* Brod. we have alternate pink and yellow bands or zones, the first sprinkled with white ocelli, the second with brown dots.

2. Components

In addition to being differentiated on a purely geometric basis, pattern elements may be distinguished on basis of «periodicity» into radial non-periodic and non-radial periodic elements [26]: this can be done because non-radial pattern elements do not appear during growth of the shell in an infinite and ever changing variety, but tend to repeat themselves time and time again. This distinction between the two types of elements has been made before by various authors (see WRIGLEY 1947, PORTMANN [no date], COMFORT 1964, etc.). In fact shell patterns might well be considered to be composed of one or both types of elements, influencing each other where they come in contact, and all often affected in various ways by

[25] In some *Neritina*, like *N. virginea* L. however, where a white blotch pattern is involved with a transversely striped one, the stripes may occasionally enclose the blotches. Where this occurs, we have a blotch within ring arrangement, though this will not be an isolated pattern configuration.

[26] We may, however, have various intermediate situations a) As indicated above, some non-radial elements may occur only once, like the converging lines at the mouths of some *Rissoa*. — b) Some oblique lines may be so nearly radial that they never leave the marginal region and never cease being secreted, even though other such lines may appear from time to time (as in *Neritina glabrata* Sowb.). The period of such lines can be considered infinite (Pl. V, fig. 15, Pl. XI, fig. 7). — c) Linear elements that oscillate about a radial axis may be oblique in their parts, but non-periodic as a whole (bands of *Tricolia pullus lineata* Mtrs.).

other features of the shell, such as sculpture, growth breaks, shape of the whorls, etc.: the pattern at any time being often also influenced by the course of its ontogenetic development, by relics of earlier secreted patterns, etc. (for ex. the vast blurred blotches in *Mitra mitra* L. are relics of the juvenile unified red field, etc.). In the matter of stability of pattern, the contrast between the stable radial elements and the generally more unstable oblique and transverse ones has already been mentioned; but even as between non-radial elements there are also huge variations in this respect: thus the zigzags of *Voluta undulata* Lam. or *Neritina reclivata* Say repeat themselves with little change, while these of *Strombus vittatus* L. are among the most protean features to be seen on any shell. Such wildly variable and irregular transverse patterns elements may, however, be relatively stable when they are associated with sculpture (as in *Rissoa lineolata* Mich., see p. 47); and in such forms as *Neritina communis* Quoy there is, especially in the last whorl, a great variety in the degree of manifestation of zigzag patterns; but once these patterns are fully developed, they are here relatively stable.

On the basis of the observation that elements, even radial ones, tend to be arranged in sets of like and generally parallel units which have presumably a common origin, one might differentiate between patterns showing only one such set (for ex. radial or transverse lines), and those showing two or more sets, or components. The latter patterns will be termed composite patterns.

It is sometimes very hard to determine the limits of a set or component, and hence the number of such in a pattern. For example in *Voluta musica* L. we have at least 4 distinct types of radial elements, the three first types each segregated in their own zones on the shell surface, the last underlying the zones containing the third. These elements are: (1) rows of dots, (2) rows of blotches, (3) lines, (4) faintly defined bands. Do we have here four radial components or four parts of one component, or neither, or both? – On examining young specimens showing the ribs, one finds, grosso modo, that the lines usually are located at the bottom of interspaces, the blotches at the top of some of the ribs, and that the rows of dots do not have a clearly defined relation to the ribbing! As the relationship of each of the sets of elements to ribbing seems to be different, and as indicated above, each is restricted to its own zones of the shell, they will here be considered as three different components, though this is admittedly only a temporary collocation. The relationship of the remaining pattern elements of *Voluta musica* L. are as follows: the bands, secreted at some depth inside the shell, are evidently associated with the radial lines, since the last always overlie the first, and on this basis might possibly be considered as being a portion of the same component. In the zones that include bands and lines are also to be found sinuous transverse lines: these at times penetrate the regions with the dot rows, and then generally are seen to run into the dots or through them, as was the case in *Monodonta articulata* Lam. (p. 13). In summary we seem to have in this shell a pattern with 4 or 5 components, but never with more than 3 in the same region. This component «count» is the highest found by the author for any mollusk.

2-component patterns are very common in the Gasteropoda, but do not show a very great variety of types. Patterns involving two sets of lines are mentioned in the chapter on secretion and also below (p. 29). Patterns involving non-radial lines or bands and radial alt. c. bands are perhaps the most common of composite patterns (Pl. III, fig. 6 d). Such a pattern could really be rated as the «typical» gasteropod pattern, and has not been observed by the author outside of that class. It occurs to various extents and in different guises in a great many families (Trochidae, Phasianellidae, Cassidae, Naticidae, Strombidae, Cymatiidae, Purpuridae, etc.). Patterns like the preceding but where the radial band is homogeneous, are decidedly less frequent, but are still found in a number of species (*Conus generalis* L., *Voluta scapha* Gm., etc.).

Patterns involving radial lines and transverse bands are not uncommon and seem mostly derived from association to a peculiar type of sculpture (see p. 46). Patterns of crossing oblique lines and transverse bands are much rarer, but may be seen in at least one species of *Tricolia* (*T. tessellata* Phil.). This about completes the list of the most common 2-component patterns of linear elements, but excluding patterns where one component is only vaguely or indirectly manifested (see «latent» elements p. 14).

3-Component patterns may be divided into those where 2 of the components have the same orientation (by far the most common case) and those where each component has a different orientation.

A good example of the first may be seen in the tent Cone, *C. textile* L. There the «tent fields» are arranged in intersecting radial and transverse zones, which make up 2 of the components. The third component of the pattern includes the numerous sinuous or lobate black lines whose relationships to the tents of the other components will be mentioned later (p. 28; Pl. V, fig. 8). We have here thus 2 transverse and one radial component.

In an other well-known Tent Cone, *C. aulicus* L., on the other hand, we have 2 radial and one transverse component. The tent field components are the same as in *C. textile,* but the transverse undulations are lacking, and instead appears a fine, rib-related radial component of very small «clear» spots or tents (Pl. VI, fig. 9).

In *Conus imperialis* L., we have as in the preceding Cones crossing transverse and radial zones (= components) though here the former are poorly developed and highly irregular, and both have a homogeneous coloration: they are moreover secreted mainly deep below the shell surface, except that the radial zones have also a superficial yellow portion (Pl. X, fig. 6). Alt. c. lines of two types, probably originally associated with major and minor ribs are also present. Wherever the transverse and radial zones underlie the major alt. c. lines, the «like» dark segments of these lines are enlarged and generally connect to these zones inside the shell substance (P. X, fig. 6). Here thus elements secreted deep within the shell substance may influence superficial elements. – We have here as in *C. aulicus* L. a three component pattern with two radial and one transverse compo-

nent, but here two of the components (the transverse zones and the alt. c. lines) are themselves composed of two distinct fractions.

Three-component systems where each component has a different orientation are in all cases studied associated with the phenomenon of «junction figures», and this one will thus be treated here:

In two-component patterns such as those of *Conus striatus* L. where the radial zones are interrupted and reduced to a series of blotches, the transverse bands, where they are present, will cross the path of the radial component only where this one is developed (in the present case, usually at the hind limit of the blotches, less often through the blotches themselves, and apparently never between the blotches). Blotches and bands will in this case often form somewhat arachnoid figures that might be termed «junction figures» (Pl. IV, fig. 18; Pl. X, fig. 5). This phenomenon is very similar to what was seen when transverse lines crossed alt. c. bands (Pl. II, fig. 9; Pl. X, fig. 4). Somewhat similar junction figures are seen in *Conus janus* Brug. and the Pulmonate *Drymaeus hamadryas* Phil.

A few species were observed to have three clearly defined components in three different directions; they are all Pulmonates: *Bulimulus coturnix* Sowb., *B. coquimbensis* Brod. and *Neopetraeus arboriferus* Pil.; in all these species, like in *Conus janus* Brug., but unlike in *C. striatus* L., the transverse component appears to be generally the essential one in the «figure» [27]. Here moreover, very much unlike in *C. striatus,* the junction figures tend to be exactly alike over great portions of the shell.

In the junction figures of *Bulimulus coturnix* Sowb., for ex., the three components unite in a very intricate manner (Pl. V, fig. 10). Such figures are repeated in whole or in part about 20 times over the last whorl. In these junction figures we see an oblique component (A) that joins a transverse one (DD). The radial component is represented by proximal projections from both transverse and oblique components (C_1, C_2, C_3: it is possible that the figure C_3 may include in its center another portion of oblique component). In the remarkable pattern of *Neopetraeus arboriferus,* which strikingly imitates a series of leafy stems, the «stems» represent the transverse component, «the branches» the oblique one, and the leaves swaying in the proximal direction, the radial one: to be noted that the leaves from one branch may overlap a stem of a preceding branch (Pl. V, fig. 9).

There are cases, such as networks, where in the present state of knowledge, a component «count» is impossible to achieve on a purely objective basis. Where connective lines appear between transverse zigzags, are these lines whose presence is obviously dependent in some way on that of the zigzags, but which are radial, to be considered a distinct component (Pl. I, fig. 10)? Or when we have, as in *Strombus vittatus* L., sets of lines of opposite but equal obliquity and that always seem to appear together and are thus most probably genetically related,

[27] In *Buliminus coturnix,* the oblique component appears to be the primary one in the upper whorls.

are such paired sets to be considered as two distinct components? Here the inclination will be, in such cases, to base the component system on a pure geometric basis (i. e., parallelism), until much more is known of element interrelationships, when in any case a much better system of pattern classification will no doubt be devised.

3. Networks

Networks are here defined as patterns in which elements are in contact with each other at short and more or less regular intervals, so as to enclose cells: they can be formed of lines, spots or a mixture of both.

a) Linear networks

Irregular, non-oriented «formless celled» networks with crossing lines (Pl. VI, fig. 1) have not been uncovered. As indicated below, lines in shell patterns do not generally cross unless they are members of a pair of components of opposite obliquity [28]; moreover, sources of secretion evidently do not shift back and forth abruptly, as would be necessary to produce the wavy, more or less radial lines that might appear in such patterns (see p. 7).

Irregular, non-oriented «formless celled» networks of the cellular type (Pl. VI, fig. 2; Pl. X, fig. 8) have been found in a few Pulmonates, such as *Helix aspersa* Müll., *Eobania vermicularia* [29] Müll., etc., where they are associated with a peculiar type of sculpture, most probably produced by extremely protean lobations of the mantle margin. Even there, we often do not have complete irregularity of pattern, and in *Eobania* there is in some specimens a strong tendency toward formation of a rectangular or rhombic labyrinthic pattern of the cellular type (Pl. VI, Fig. 4).

Well defined rectangular labyrinthic networks have not been found in ordinary Mollusks, but are present in some *Cypraea* of the *C. arabica* group. The networks of these species are essentially of the cellular type but may include a few crossings: and with their junction dots and two sets of irregularly developed elements at right angle to each other, they offer a close rectangular equivalent to the rhombic pattern of some specimens of *Strombus vittatus* L.

Rhombic labyrinthic networks will be mentioned below in connection with overlapping triangular patterns.

Overlapping networks are oriented in all the species studied.

Overlapping irregular formless patterns, such as figured on Pl. VI, fig. 6 have not been found, but close approximations thereto may be noticed in some *Conus aulicus* L., where the rather irregular tear-shaped clear areas tend to crowd and partly fuse with each other.

[28] To be noted that «opposite obliquity» as employed here does not necessarily mean opposite and equal obliquity.

[29] As the pigment deposited within the ribs, or rather the swellings, of *Helix aspersa* is white, the network will be by the present definition (p. 17) be a network of the «reverse» type (colourless frame surrounding coloured cells).

Of all the overlapping irregular patterns, the triangular one is probably the most commonly found. In almost all cases, where the pattern is fully developed, the triangles, «tents», «japanese mountains», have their apex oriented distally (*Oliva porphyria* L., *Voluta imperialis Lam., Lioconcha lorenziana* Dillw., etc.: Pl. XI, fig. 9). This orientation of the patterns derives from the fact that here: (1) There is much branching off of lines from other lines (lines s, s', s", from AB, Pl. VI, fig. 10 [1]). (2) When two lines (= two sources of secretion) meet, they will tend both to stop right there and then [30]; and also at least in some individuals of *Oliva porphyria,* from (3) an abundance of simple converging patterns. – To produce a pattern of that type oriented proximally, there should be (4) an absence of branching; and (5) when two lines meet one should continue on its course (see «inflowing», p. 9: when in Pl. VI, fig. 10 [2], lines s, s', s" reach BA, this line continues to be secreted); (6) there might be in addition a number of diverging patterns. – No clear case of such an orientation has been noted (though poorly developed patterns in some *Tapes litteratus* L. may approach it), and this is due perhaps to the rarity of phenomenon (5). Where these two orientations are about equally balanced, one would expect to find rhombic labyrinthic networks: such are developed to an extent in some Veneridae, such as *Sunetta meroe* L. (Pl. X, fig. 10) and an unidentified *Anomalocardia* (Pl. VI, fig. 8). Tent patterns pointing upwards and downwards have not been found, probably because of the fact already noted that sources of secretion do not normally shift back and forth.

In many Cones (*C. aulicus* L., *C. textile* L., *C. omaria* Brug., etc.) «tent patterns» may be observed that look superficially rather similar to those of *Oliva porphyria* L., but seem to bear no relationship to zigzags. The derivation of the «tents» is here evidently from ogive shaped, colourless areas in the pigmented ground. Each of these «light» spaces widens rapidly to a maximum, and then narrows gradually to its end (Pl. VI, fig. 9). Around the distal portion of these «ogives», where they narrow, the pigment often tends to accumulate, forming there a dark rim, just as if the secretory cells, after a period of inactivity, were overfilled, and released at once all the excess colouring matter. When such «ogives» are produced close to each other and become adjoining or overlapping, a «tent pattern» appears (Pl. VI, fig. 9). Here however the «tents» are ogive-shaped rather than triangular, as in *O. porphyria* L. and it is no doubt the shape of the original «light» spots and the mode of their overlap [31] that determine here the distal orientation of the tents. – In *C. textile* L. these «ogives» are involved in a rather surprising way with a pattern of transverse undulous lines. The pigment of the lines fuses with that around the ogives, where these patterns meet, in extremely diverse manners (Pl. V, fig. 8).

[30] Factors (1) and (3) also define the main differences between a «tent» pattern and one of zigzags. Zigzags do not involve any branching and show the same number of divergences and convergences.

[31] If the ogives were to overlap proximally we would have a proximally directed scaly network.

There are all kinds of gradations between tent patterns of the Cone variety and scaly networks that are formed from lobes, these latter having the same origin as the ogives above mentioned. Because of this origin, the scales have always been found oriented distally (as in *Conus tigrinus* Sowb., *C. abbas* Brug., etc.). Scaly networks may be variously irregular in both arrangement and size of scales, or may be regular as in portions of *C. abbas,* where they may grade into regular rhombic networks (Pl. VI, fig. 13).

Regular (relatively!) networks of rhombs and parallelograms are, with the checkerboard pattern mentioned below, the most common type of regular networks on the molluscan shells. Such rhombs might theoretically easily be produced: (1) by the crossing of two sets of lines (Pl. I, fig. 11; Pl. X, fig. 9), (2) by adjunction of alternate zigzags (Pl. I, fig. 10, AB–CD), (3) by joining together parallel zigzags with connective lines (Pl. I, fig. 10, AB–EF)[32]. As indicated in the chapter on secretion, all three methods of network formation are to be found on actual specimens, especially in the Strombidae (*S. vittatus* L., *S. canarium* L., *S. succinctus* L., etc.), Littorinidae (*L. fasciata* Gray, *L. zigzag* Gm., etc.) and various other families. It appears that regular rhombic or parallelogram-celled networks of any extent are usually composed of (1), though, since the two crossing sets of lines often make their appearance as prolongation of zigzag limbs, a clear distinction between the various methods of rhombic network production is not always easy to make. Of these two sets of lines, each may partially dominate over some region of the shell surface; where one set is strongly developed, the other set may be represented merely by junction spots (Pl. VI, fig. 11).

In reason of the presence of these junction spots, the rhombic networks are actually in a pure sense networks that include both lines and spots (Pl. VI, fig. 11); and as the usually more or less rectangular spots generally cut off a bit at the end of each rhomb, these latter might be regarded as octogons. In fact there are all kinds of intergradations from spots whose dimensions in regard to, and effects on the rhombs are insignificant, to those that lead to the production of authentic, though elongate octogons (or hexagons if only two of the spots are strongly developed), and finally to spots that are so well developed that little is left of the sides of the rhombs and we get a checkerboard pattern (Pl. VII, fig. 22).

Rhombic networks may be produced, in addition to the above, by means which might be less easily imagined: (1) Through joining together of the dots of a dotted pattern, as in *Tricolia pullus* L., *T. speciosa* Mühl., *T. affinis* C.B. Ad., *Mitrella lalage* Phil., etc. In all these cases the lines of the network tend to be rather indistinct, and they may simply result from a «nearness effect» between the closely spaced dots (Pl. V, fig. 1); (2) Through widening or multiplication of light spots in ocellated and like patterns, wherever such a spot will have four close neighbours

[32] Rhombic patterns could also theoretically be derived, as in Pl. VI, fig. 16 from the joining together of tips of adjacent zigzags. The fact, that connective lines join only the parts of succeeding zigzags closest to each other (p. 10), may explain the lack of such pattern on shells.

in the oblique directions (ex. in *Theodoxus fluviatilis* L., *Anachis avara* Say). When these spots adjoin on all sides, a rhombic (more or less) network will automatically result (Pl. VI, fig. 17)[33].

In *T. fluviatilis* L. the spot arrangement appears to be an irregular variety of the crossed-oblique type (see p. 22)[34]. In *Anachis avara* Say a radial arrangement seems to be predominant on some parts of the shell, but the spots in adjoining radial rows still have a tendency to alternate [35]. (3) Through modification of other types of networks, like the scaly networks of *Conus abbas* Brug., or the «egg and trapeze» network of *Conus marmoreus* L. (A in Pl. VII, fig. 12).

WRIGLEY (1947, p. 211) was the first, to the author's knowledge, to have noted the derivation of a rhombic network from zigzags, though the network in question concerned sculpture and not colour pattern (sculpture of the fossil clam *Textivenus*). NEUMANN (1959) described the peculiar network of *Theodoxus fluviatilis* L. and noted its relation to the spotted pattern.

Parallelogram-celled networks and isolated parallelogram-shaped cells are often associated with regular rhombic networks, especially of the crossed-lines type. In general, in such patterns, rhombic networks result when the lines of the two sets have exactly the same frequency of occurence, while parallelogram-celled networks result when the frequency is different for the two sets (as in parts of *Littorina fasciata* Gray, *L. zigzag* Gm., etc.: Pl. X, fig. 7).

A much less regular parallelogram-celled network is found in portions of *Tricolia tessellata* Phil., where we also have two sets of crossing lines, but here the obliquity of the two sets is very different, and especially the lines of the near-transverse set are discontinuous (Pl. II, fig. 5).

Regular triangular networks could theoretically be produced like the rhombic ones from zigzags, but there would in addition have to be intercalation of periodic transverse straight lines at precisely the right places to ensure splitting of the rhombs in half (Pl. VI, fig. 4). Occurrence of such an intricately regular pattern would indeed be surprising, and nothing like it could be detected on any specimen.

[33] If the spotted field were entirely regular, we would get squares instead of rhombs.

[34] In *Theodoxus fluviatilis* L. these light spots are very elongate, and like the «ogives» of *Conus omaria* Brug. mentioned above (p. 18) have their distal portion circled by an accumulation of pigment. It is this pigment, which here forms the sides of the rhombs when these appear (Pl. VI, fig. 15). The pattern of *Septaria janelli* Recl. is like that of *Th. fluviatilis* L., but much drawn out in length. Such drawn-out patterns are also seen in zigzags, such as those of *Terebellum terebellum* Lam. var.

[35] There might at first sight seem to be a complete range of variation from spots to networks to ocellated patterns, to wit: fields of spots (*Tricolia pullus* L.); spots connected by faint lines (*T. pullus*); spots connected by pronounced lines (*Strombus vittatus* L.), forming a fully developed network; networks in which the cells are partly filled with pigment («egg and trapeze» network of *Littorina meleagris* Pot.); isolated clear spots, as in *Nitidella ocellata* Gm. Only the second portion of this gamut of variability appears to be valid, all stages from network to ocellated field being present in various species, such as *Anachis avara* Say. The faintly marked network of *T. pullus,* on the other hand, was not observed in any specimen to develop into one with a strongly marked framework.

Regular hexagonal networks may be produced theoretically from zigzags and trapezoid crenations (Pl. VI, figs. 20, 22, 23). In actuality their modes of production are even more varied than that for rhombs. The following origins of hexagons and hexagonal networks have been noted:

(1) From transverse zigzags and connective lines, as in the *Strombus vittatus* group, a number of Cones, including *C. pyramidalis* Maury, etc. (Pl. VI, fig. 23, upper part; Pl. XI, fig. 5). Here the hexagons will have apices at their proximal-distal extremities.

(2) From the crossing of two sets of zigzags of opposite and (more or less) equal obliquity, producing hexagons oriented as above, as in *Littorina meleagris* Pot. et Mich. These lines of opposite obliquity producing the hexagons are usually straight where they do not cross (Pl. VI, fig. 22, bottom; Pl. XI, fig. 1, to left), and become zigzagging only where they do so, the zigzags having oblique and radial limbs (Pl. VI, fig. 22, AA, BB etc.). Such lines might be considered as offset where they meet and the phenomenon may be similar to that of the offset instable elements in *Conus generalis* (p. 12) except that here the «stability» of both crossing elements is exactly equal. Why there should be such offsets here[36], with production of hexagonal networks, and not in *Littorina tessellata* Phil., where parallelogram-celled networks are produced, is not too clear.

(3) Some hexagonal cells with sides instead of apices at the proximal-distal extremities were noticed in *Conus pyramidalis,* and are produced from zigzags with transverse and oblique limbs, and connectives. Similarly oriented hexagons may result when, as in some *Nassarius corniculum* Oliv., a system of crossing lines becomes involved with alt. c. bands.

(4) Hexagons oriented in the same manner may be produced from trapezoid crenations. Such crenations may be seen in the juvenile *Bulla striata.* They are apparently derived from an association of transverse sinuous lines with alt. c. bands with linear «like» portions (p. 40; Pl. VI, fig. 20). It seems that the hexagonal network may be derived both from parallel, close set trapezoid crenations, joined by connective lines and alternating crenations that meet at the angulations.

(5) Hexagonal networks, like rhombic ones, may also be produced by expansion of light or colourless dots from an ocellated pattern. In *Nitidella ocellata* Gm. (Pl. X, fig. 11), each dot often has 6 close neighbours: the four ones in the oblique directions, as in *Theodoxus fluviatilis* L., but also a pair in the transverse direction (Pl. VI, fig. 18). When all these dots expand, there results a hexagonal network[37]. When the 6 closest neighbouring dots are in the oblique and radial

[36] Even in this species the lines are by no means always offset, and we may have perfectly respectable rhombic networks in number of individuals.

[37] The hexagons derived from expansion and/or multiplication of ocelli until they adjoin on all sides, may not be as «new» as they might appear, at least in *Nitidella ocellata;* for the available specimens show early growth stages with a fully developed hexagonal network, that vanishes later on. This hexagon formation in the adults of some individuals may thus merely represent the gradual reemergence of the juvenile pattern from the dark homogeneous «ground».

directions, we will have, when the dots expand as before, a hexagonal pattern, but with hexagons oriented as those in *Bulla striata* (Pl. VI, fig. 19). A few cells of this type have been detected in *Anachis avara* Say [38].

(6) Finally, hexagonal networks, like rhombic ones may be derived from lobed patterns. In the present case the lobes of one row are secreted at some distance from those of the preceding row, the sides of the lobes abut and interfere with each other (p. 33), and we get there straight lines that form the upper and lower sides of hexagons (as in *Conus abbas* Brug., Pl. XI, fig. 2, center of specimen). The lobes of a row may unite to form lobed lines; where the lobes of successive lines alternate, connecting lines may develop between the rows, and we also get hexagonal networks (as in *C. geographus* L.).

Regular octogonal networks of a sort may be produced when the junction spots of rhombic networks become big enough, as indicated above. Such a network, strictly speaking, even much more so that the rhombic network, is a network of lines and spots, and in any case never appears in anything more than a few cells at a time. Regular linear octogonal networks are of course a geometrical impossibility; and purely linear networks of mixed octogons and rectangles (derived from trapezoid crenations), though theoretically possible, could not be found on any specimen.

Regular trapezoid networks could theoretically be derived from hexagonal patterns of type (4) by means of transverse lines (Pl. VI, fig. 21), just like the equally theoretical triangular network from a rhombic one (Pl. VI, fig. 14). No actual case of such a phenomenon could be detected.

Having examined the regular networks that could be produced from straight lines, zigzags and crenations, it might be of interest to see what network, if any, can be derived from sinuous or lobate lines. From the first, two possible types of networks might presumably be produced: with the undulate lines crossing at right angle (Pl. VII, fig. 10) not, it appears, a very promising possibility; or with the lines parallel, alternating, and connected at the summits of the curves (Pl. VII, fig. 9): this pattern, which corresponds to the rhombic network produced by contacting zigzags, is realised magnificently in *Neritina piratica* Rus. (Pl. XI, fig. 4). – Lobate lines give the two possible networks figured on Pl. VII, figs. 13, 11, namely the «scaly» network produced by contacting alternating lobate lines and the «catenate» network, with a higher degree of symmetry, where the lobes are paired face to face and back to back (Pl. VII, fig. 11). Scaly networks are found in many Cones, but appear in all cases to be formed of single lobes [39], not

[38] Virtually all possible means of hexagon production from simple elements are thus utilized in nature, except that from radial zigzagging lines, but such lines have never been found by the author on the shells of Mollusks.

[39] Since in *Conus abbas* Brug. the scales involved in the rhombic network have an angulated shape, that network might be considered as being made up of convergent angulations, were it not for the evident relation between the regularity of the network and the angularity of the scales! Rhombic networks derived directly from simple angulations have not been detected anywhere.

of lobate lines. Fully developed catenate networks have nowhere been detected, though isolated «chains» and links thereof have been found in two species: in *Philine catena* L. the chains, remarkable enough features, are fully developed but isolated from each other and, despite appearance to the contrary, pertain exclusively to the sculpture, not the pattern; in *Phasianotrochus bellulus* Dunk., the colour pattern is involved, but there the chains, also isolated, are reduced at most to a few links. Finally a network combining crossed lobed lines and straight lines is theoretically possible (Pl. VII, fig. 14), and is represented in rather irregular form in *Tricolia tessellata.*

b) Networks made of lines and spots

Unter this heading will be considered those networks in which the junction spots are particularly well developed. As indicated above, such is frequently the case in ordinary «rhombic» regular networks. Perhaps the most characteristic lines-and-spots network, however, is the one labelled here «egg-and-trapeze» network, strikingly developed in *Conus marmoreus* L. and numbers of *Littorina meleagris* Pot. et Mich.; in both cases, the «eggs» of the network are the colourless areas, the «trapezes» the junction spots.

In *Conus marmoreus* L. this pattern is to all evidence developed from an ocellated pattern: these «eyes» have here, as they usually do, an ogive to ungulate shape, with the blunt end proximal. The egg-and-trapeze network here seems to represent the pattern that would automatically be developed, when such ogive-shaped light spots arranged in oblique rows are as close together as they possibly can, without impinging or overlapping on each other (Pl. VII, fig. 12). When some overlap occurs, we may get a «shield-and-arrowhead network» (fig. 12, B). When the spots abut on each other, and apparently interfere with each other, we get a rhombic network (fig. 12, A)[40].

In the case of *Littorina meleagris* Pot. et Mich., the egg-and-trapeze network appears to be derived[41] from a rhombic network in which secretion fills the distal

[40] The ocelli in a ocellated pattern may have five types of interrelationship (P. VII, fig. 12): (1) They may be isolated from each other (fig. 12 E); (2) they may touch (or rather the space between ocelli may be reduced ot a line), without overlapping on or interfering with each other (fig. 12 upper portion); (3) they may overlap (that is, the proximal overlap on the distal (fig. 12 D); (4) they may abut and «interfere» with each other (fig. 12 A); (5) they may fuse partly or along their entire length (fig. 12 between c and c'). When a proximal spot overlaps on a distal one, the shape of the first is not modified thereby; when the spots abut and interfere, the common border or rim tends to become a straight line between the limits of the contacting zone; when they fuse, the «ocellus-rim» that usually tends to bound the ocellus at its distal end breaks through. — The interrelationship (2) will give egg-and-trapeze networks, (3) distally pointing tent-and scaly patterns, (4) rhombic and hexagonal networks. Virtually all of these interrelationships and resulting patterns may be found in the different varieties of *Conus marmoreus* L.

[41] How to distinguish derived from original patterns may on occasion be difficult, especially as the juvenile stages of specimens are often lacking in collections. 3 main criteria (depending on what specimens and portions of specimens are available) have been used here

part of the rhombs, as well as all angulations (Pl. XI, fig. 8, center). In such networks, unlike in that of *Conus marmoreus,* the blunt end of the «egg» is distal, as is the summit of the «trapeze». When half the rhomb is filled with secretion, we may get triangular checkerboards (Pl. VII, fig. 18 at left).

Irregular networks made of lines and spots (Pl. VII, fig. 7) would amount to irregular cellular networks with irregular or regular spots at the junctions: though theoretically possible, such networks have not been detected anywhere.

c) Networks made of spots [42]

ca) Spots adjoining: «reverse» networks. – Networks in which the usual colour arrangement is reversed (i. e., the cells pigmented, the frame light), would appear of difficult realization in view of the «nearness effect» (p. 15), and yet coarse-meshed «reverse» networks have been found in a few Gasteropods. The peculiar case of *Helix aspersa* Müll. has already been discussed; the other reverse networks mentioned here will be regular networks.

In *Terebra dimidiata* Lam. we have about 1 1/2 rows of cells of a coarse-meshed rectangular reverse network. It seems evident that the frame is the primary or «active» element, the spots being only portions of the «ground» isolated by two sets of light bands crossing each other at right angle (Pl. XI, fig. 3).

In *Babylonia ambulacra* Sowb., and to a much lesser extent in other species of the genus, is to be found a truly remarkable hexagonal reverse network, unfortunately somewhat «dim», in reason of being secreted rather deep within the shell substance. The hexagons, though generally elongate, may, apart from this, be quite regular: here also the «frame» appears to be the primary factor. Though the genesis of the pattern is not too clear on the three available specimens, it does appear that we have originally transverse light bands which seem to develop into zigzags under the influence of rows of radial bands that are secreted between them, and in alternating positions between successive transverse bands (Pl. VII, fig. 19; Pl. XI, fig. 6).

cb) Spots alternating, usually in contact at their tips: checkerboard networks. Polygonal spots of only two types can produce, or at least be involved in regular checkerboard networks: triangular (triangles) and quadrangular (squares, rectangles, rhombs, parallelograms and trapezes).

In the Venerid Pelecypod *Lioconcha tigrina* Lam, and in *Neritina piperita* Ch. there is at times a tendency for the coloured triangles of their patterns to cluster

to determine the original pattern: (1) Earliest appearance, the best criterion of all, when it can be used; (2) Most common distribution in the phylogenetic group involved, especially in the juvenile specimens of that group, if any are available; (3) Simplest configuration on the specimen. — The aspect of the pattern on the upper and lower parts of the whorls may also provide some clues as to the genesis of that pattern on the main whorl portions.

[42] Made of «spots» only from a purely geometric point of view, in the case of reverse networks. As indicated in this chapter, the frame seems to be the primary factor in reverse networks as in the others.

together, but never in the available specimens to form true triangular checkerboards. In the first species the triangles tend to fuse in both oblique and lateral directions, in the second they fail to touch regularly. – True, «honest to goodness» triangular checkerboards, with the sides of the «triangles», however, generally slightly convex, are produced with «egg-and-trapeze» networks in *Littorina meleagris* Pot. and Mich. (Pl. VII, fig. 18; Pl. XI, fig. 8).

Rectangular checkerboards are probably the commonest of regular networks and may be found among the Rissoidae, Strombidae, Littorinidae, Phasianellidae, etc., and in at least one common species of Pelecypods. They may originate in at least three ways:

(1) Like rhombic networks, from zigzags and crossing lines, but in this case the junction spots are the most prominent feature of the network, and indeed may alone be present, as on numbers of *Rissoa guerini* Recl. If one admits that, as indicated before (p. 10), pigment secretion in such cases tends to be concentrated on the junction spots that would otherwise be laid down along the original elements (lines and zigzags), then where these original elements become as wide as the intervening clear spaces the junction spots will greatly impinge on these narrow interspaces, tend to become connected with each other, and some kind of rectangular checkerboard will automatically result. There is thus actually no essential difference between such checkerboard networks and regular rhombic ones, and all intergrades between the two may be seen in *Strombus vittatus* L. and *Rissoa guerini* Recl. (Pl. VII, fig. 22).

Junction spots relatively much bigger than this, that would partly fuse with each other have not been noticed, perhaps because in such a pattern the clear spaces would have to be too narrow to actually appear, in reason of the «nearness effect».

(2) By the breaking up of closely spaced zigzagging or oblique «lines» or bands into rectangular units (Pl. VII, fig. 21), so that units of one band will come into contact with those of the next. This may often be seen in *Rissoa guerini*. The process is not markedly different from (1), from here too secretion otherwise distributed all along the lines tends to be concentrated in a number of rectangular segments: the segments in the present case will usually stay connected to each other by thin lines, perhaps a result of «nearness effect». Less regular checkerboards but apparently with a similar origin may be found in the Pleurodont Pulmonate *Solaropsis pellis-serpentis* Chemn. and especially in the Venerid *Macrocallista maculata* L., where indeed the «rectangles» are often merely trapezoid blotches which, like blotches in many other Pelecypods, are distinct apically and fade out distally. A variety of this mode of checkerboard formation is obtained when fragmentation of the bands is evidently due to a strongly defined sculpture, such as the grooves of *Littorina tessellata* Phil. Since the rectangles across such grooves will tend to have unrelated positions, the checkerboard will result more from chance than from anything else and will not be as regular as those of *Rissoa guerini* Recl.

(3) Sculpture and especially grooving seems to influence other types of patterns into producing checkerboards. For ex. the ocelli of *Nitidella ocellata* Gmel. become modified to rectangles or squares between the grooves of the ribbing on the shell base, and when closely spaced, form with the dark intervening spaces a rectangular checkerboard.

Networks made of irregular spots are hard to obtain, for the very fact that the spots are irregular will make it unlikely that they will be separated from each other by a uniformly thin «frame», or that they would always be in contact with each other at whatever tips they happen to have (Pl. VII, fig. 16). Such spots (as in *C. generalis* L., for ex.) would either partly fuse with each other or not be in contact at all and we would get an irregular blotchy pattern, not a network.

4. Sundry pattern types

Composite patterns have been defined earlier as those that have two or more components. Networks are almost invariably composite.

Complex patterns may be defined as composite patterns wherein the relationship between components is not simple (as in *Phasianella speciosa* Mühlf., and in *Conus textile* L., see p. 25) – in ordinary composite patterns this relationship is more or less easily discernible at a glance (as for the radial and concentric bands in *Busycon contrarium* Conrad).

Irregular patterns would be those where the arrangement of elements and the elements themselves are irregular. This is to a great extent the case for the blotched pattern as such of the adult *Bulla striata* Brug., or the white irregular network of *Helix aspersa* Müll. as such [43].

There may be irregular patterns where the elements, though irregular and irregularly distributed, yet show a characteristic orientation: such as the irregular transversely banded pattern of *Neritina smithii* Gray, or the irregular transversely zigzagging pattern of some *Strombus canarium* L.

A confused pattern is one which is so complicated that one does not know at first, what one is looking at: examination of pattern ontogeny shows, in most of the cases studied in this respect, that the confusion results from the fact that two distinct patterns are superimposed on each other; in many cases an adult pattern is partially superimposed on a juvenile one, or partially replaces it: in *Bulla striata* Brug. for ex. the rather irregular blotched pattern mentioned above is partly superimposed on and partially replaces a relatively regular hexagonal network. A somewhat similar situation apparently obtains in the case of some *Terebellum terebellum* Lam. In some undetermined *Umbonium* there is a continual splitting of alt. c. bands, but this splitting is often not complete and portions of the old

[43] Actually in *Helix aspersa* Müll. the basis for the irregular pattern is an irregular network of swellings which are filled with white pigment when they lie within the paths of the transverse and radial bands of a composite colour pattern. The shell substance underneath the swellings is also very light in the radial and sometimes in the concentric bands.

wider bands may remain associated with the newer bands. And in the adult *Strombus vittatus* L., as indicated p. 10, two sets of oblique lines may partly or wholly replace the original transverse zigzags.

An indistinct pattern is one that is hard to make out because: (1) the pigment is either too light, or not markedly differentiated from that of the ground; (2) the pattern is secreted deep inside the shell and thus does not show clearly on the outside thereof (or on the inside, for that matter, since it is covered with the inner shell layers). – Indistinct patterns of both types may be seen in various species of *Oliva*.

5. Periodicity

a) Introduction

Two observations will here be recorded concerning this topic: (1) Periodicity is to all appearance never perfectly achieved, for pattern elements never repeat themselves exactly; (2) Periodicity may be of several degrees, of which the following appear theoretically the most notable: (a) Simple repetition of a type of activity of secretion sources (for ex. repetition of a divergence of sources [Pl. V, fig. 13 b]); (b) Regular repetition of such activity (fig. 13 a); (c) Regular or irregular repetition of this type of activity on the same portion of the margin (fig. 12 a and b); (d) Repetition, with various degrees of regularity of a complex serie of interrelated activities along the whole shell margin (as for the parallel sinuous lines of *Neritina reclivata* Say).

Degree of periodicity and the perfection thereof are sometimes hard to compare from one type of element to another, and especially as between «small» elements and «big» ones. The theoretical pattern of Pl. V, fig. 11 seems to show a lower degree or type of periodicity than the pattern of fig. 14 and yet the reverse is the case: for the diverging lines of fig. 11 always stop being secreted at the same distance (= same time interval or period) from their origin, while the otherwise identical diverging lines forming the pattern of fig. 14 continue to be secreted until they meet the neighbouring lines, without regard to periodicity.

b) Periodic variations

The period of secretion of the pattern elements (e. g. of successive transverse lines) may theoretically vary from one place to another, in all directions: radially obliquely, transversely, irregularly, with the variations gradual, abrupt, periodic or irregular. Actually only a rather gradual, irregular variation of periodicity could be observed in the radial direction, for ex. in the case of the undulous transverse lines of *Tricolia pullus* L. In the transverse direction however, we find a great variety of periodic changes. In *Neritina glabrata* Sowb. (Pl. XI, fig. 7) we have at the top of the whorl very numerous, almost transverse lines, indicative of short periods: the rest of the whorl is covered with almost radially oriented lines, with obviously a great lapse of time between the appearance of any two lines (Pl. V, fig. 15). The change from one pattern to the other here is abrupt, and the

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:

(1) Independent type: Element 1 bears no evident relationship to element 2
(2) Subordinate type: When element 1 vanishes, 2 disappears
(3) Associated type: When element 1 vanishes, 2 remains unaltered
(4) Correlated type [47]: When element 1 vanishes, 2 changes.

In all the cases studied, element 1, or the primary element, was taken to be the sculpture (esp. the external ribs), as it seems to influence the pattern or elements thereof, without being influenced by it, and also appears in general more stable than the pattern.

(1) Independent type. This type includes almost all the colour patterns and pattern elements which are not oriented as the sculpture, and some with the same orientation. It appears evident that though the outline of the white transverse zigzags of *Columbella fulgurans* Lam. may be influenced locally and in a minor degree by the radial ribbing, these pattern features as such are quite independent of that ribbing; the same applies to the radial rows of spots in *Mitra mitra* L. and the radial bands of *Terebra subulata* Lam., whose limits do not correspond to those of the radial sculpture elements.

In many cases, one has a pattern to all appearance independent of the ribbing in regard to its origin and general aspect, and yet as indicated above for *Columbella fulgurans* Lam., clearly influenced by that ribbing. This influence may affect the shape and/or shade of the colour patterns. In *C. fulgurans* local jags (embayments and projections) in the zigzags are seen to coincide with the ribs and interspaces of the radial sculpture (Pl. IX, fig. 4). These jags do not follow the trends of the growth lines, so it is clear that the influence there is that of the ribbing itself.

Another ribbing effect is the differential shading that it often produces in the patterns that traverse it. A good example of this phenomenon is seen in many individuals of *Arca zebra* Swains., where the chevron-shaped stripes are darker on the ribs than in the interspaces; a probably similar factor is operative in *Conus striatus* L. though there the denticles and indentations are usually better developed than the outside ribbing and may be mostly responsible for the light and dark stripes on the irregular transverse bands.

(2) Subordinate type. Here the very presence of the secondary element seems to depend on that of the primary, though the reverse does not appear to be true. The most striking examples of subordinate elements are the various features of a varix which appear to exist only in the presence of the varix itself: thus the rows of spines of *Murex tenuispina* Lam., the dark radial stripes on the varices of *Harpa nobilis* Lam., the dark colouring in front of the «internal varices» of *Pyramidella maculosa* Lam., etc. In all these cases, the secondary element could theoretically be lacking (and in the last named species appears occasionally so to be [48]. There is a special sort of subordination which could be termed «necessary

[47] The elements termed here «correlated» were called «dependent» in the author's 1966 work. That latter term, however, has already had prior usage in the German «school» of conchology (see NEUMANN, p. 405: abhängig), to designate a quite different type of phenomenon, and is thus here discarded.

[48] The «subordinate» phenomenon shows some similarity to that of «influence» (see above paragr.) and there might be cases where it would be hard to establish which one one had. In general «influence» is here considered as a secondary phenomenon in interelemental rela-

subordination», e.g., the relationship in *Natica* of funicle to umbilicus: if there were no umbilicus there could be no funicle!

(3) Associated type. When the primary element with which the secondary is associated positionally and otherwise, vanishes, or looses direct contact with it, the secondary maintains itself as if the primary element were still there. Here are to be included most of the radial lines and bands associated with ribbing of the same trend, which maintain themselves in the same position on the whorl face, whether this ribbing be present only in the juvenile stages and later vanishes, or whether it remains throughout shell growth. Examples worth citing might include the white radial lines of *Harpa major* Röding, the dark lines of *Alectrion glans* L., *Fasciolaria hunteria* Perry, etc. It might be added that a distinction between this type of element and the next is generally made possible only through disappearance of the primary element (ribbing mostly), on observing how the secondary element is affected; such a distinction is thus difficult to achieve in wholly ribbed shells, except by analogy with other similar shells and elements.

A remarkable example of association is that of warts with ocelli in *Neritina squamosa* Sowb. (Pl. IX, fig. 6). Many specimens of that species, and even more of related species of *Neritina,* such as *N. pulchella* Recl., have ocelli with lobate distal rims, the latter often with peculiar eyelash-like extensions (Pl. IX, fig. 5); these ocelli have a somewhat irregular crossed-oblique distribution (see p. 22). In most *N. squamosa* Sowb. available, a wart appears under each ocellus, with the rim usually to be found somewhere on the wart-slope (Pl. IX, fig. 6). Often the oblique and transverse alignments of the ocelli are emphasized by ridges: on such ridges the warts may be poorly developed or even absent. The ridge pattern may in places have an appearance rather strikingly like that of the partly reticulated zigzags on some *Strombus vittatus* L., illustrating once again the evident kinship of the crossed-oblique distribution and the rhombic network patterns. The «associate» relationship of warts and ocelli is demonstrated by the fact that the first may appear fully developed on homogeneously coloured shells and the second will remain fully developed and unmodified even on parts of the whorls where warts are lacking. The present wart-ocellus relationship is interesting in that it indicates that this associate relationship is not limited to radial elements.

(4) Correlated type. This type of element was the one termed «dependent» in the author's 1966 paper. Its essential character, in so far as can be ascertained, is that while the primary element and it are both present, it will, in its typical form maintain a very stable position in relation to the primary element, and indeed generally also to the shell as a whole [49]. As soon however as the primary element

tionships, as in elements independent of ribbing in origin, orientation, etc, yet being secondarily influenced by it. Subordinate elements to all evidence can exist only in association with ribbing, etc.

[49] This effect, at least apparent, of the primary element on the correlated element, recalls the phenomenon of influence: influence, however, typically affects elements not otherwise connected to the «source» of influence.

disappears or looses its connection with the correlated element, this latter one will tend to become modified, to shift its position, etc. often in a highly irregular manner.

In effect, thus, it looks as if the association of subordinate and primary element were generally total, and often necessary; that of the associate element complete in respect to position, while in the case of the correlated element, there appears to be fundamentaly only a very approximate and general correspondance in position with the primary element, and evidently only some influence of the latter, direct or indirect, makes it appear as if this correspondance were much closer. It could be that the essential difference between associated and correlated element is simply the greater stability of the former, but with the limited amount of evidence at hand this appears impossible to assert.

An excellent example of correlated type of pattern elements may be found in *Pusia tricolor* Gm. (Pl. IX, fig. 7; Pl. XI, fig. 11). In the juvenile stages of that species, the transverse ribs are white (or rather are overlain by white bands), and the interspaces brown. A radial white stripe transects both bands and ribbing, connecting the transverse white bands with each other. As the ribbing grows fainter and finally vanishes altogether in the adult shell, the white transverse bands become more and more irregular, may extend into the brown bands to the point of splitting them into islands, this whole zone of alternate white and brown bands showing a most confused and complex pattern (Pl. IX, fig. 7, last whorl). The transverse white bands are of course here the correlated element, the radial white stripe a stable element unrelated to any sculpture and maintaining itself unchanged in the adult stages. – It may be added that here the frequency of occurence of the white and brown transverse bands is less variable than their shape.

Another example shows both correlated and associated elements in a single pattern, and the way both these elements evolve: the juvenile *Fasciolaria hunteria* Per. shows white transverse swellings and brown radial grooves. In the adult both swellings and grooves vanish, but the white transverse areas have multiplied, and become completely irregular, while the brown radial lines originally in the grooves maintain unchanged their original aspect and position on the whorl.

In the following examples, associated and correlated elements do not appear together, but one after the other: in the first case correlated elements appear first; in the second, presumably correlated elements show up last.

In *Mitra papalis* L. the juvenile stages show transverse swellings on the distal side of growth interruptions. These swellings are here white, the rest of the whorl (at least above the suture) red with a few transverse white bands in addition to those on the swellings [50]. Radial ribs are present but are not coloured differently from the rest of the whorl. What is seen therefore at this stage, is a pattern of transverse white bands irregularly correlated with similarly oriented swellings. In the adult, the red colour disappears, except on the ribs, where it persists as rows of

[50] There are thus at least two types of irregular combinations: one in which the secondary element is to be found with the primary only part of the time, the other in which the secondary is always found with the primary, but also outside of it.

spots conformable to those ribs. The swellings also vanish and the white transverse bands become indistinguishable from the white ground of the shell. In the adult stage of this species therefore we end up simply with a pattern of radial rows of red spots associated with the ribs.

In most *Planaxis lineatus* Costa, the brown bands on top of the radial ribs of the juvenile form persist unchanged in the ribless adult, and are therefore typical «associated» elements. In a certain fraction of individuals however, this pattern is present only in the young: in the adult, generally following on what appears to be a break in the shell, a completely different pattern is produced, consisting of very irregular and multitudinous radial lines and stripes (Pl. XI, fig. 10); only at the very bottom of the whorls, where the ribbing persists, do the lines, conformable with it, show some regularity. A preliminary conclusion would be that in such shells, an accident produced an alternation of colour pattern, and that this new pattern appears to be of the correlated type. It must be added that in rare shells the typical associated pattern does not appear, only the supposedly correlated one; and this one only in the later growth stages of the shell.

In some shells we have what might be called irregularly correlated elements. In *Rissoa grossa* Mich. and *R. lineolata* Mich., the elements in question, transverse brown lines, run down the interspaces of a transverse ribbing (Pl. IX, fig. 8): sometimes these lines are sinuous even within the interspaces, occasionally so much so, that the curves may extend onto the ribs: often too, the periodicity of the lines is different from that of the ribs, and we may have two lines per interspace, one on each side thereof: we thus see here no perfect conformity of lines and ribbing. – At about the middle of the whorl, where the ribs end, the lines usually become much more irregular and sinuous and either change markedly in direction, or shift strongly only to pursue later a course more or less similar to that followed in the upper part of the whorl (Pl. IX, fig. 8), or both shift and change direction. It is as if the presence of the ribs tended to confine or channel the lines along the interspaces in a course parallel to the ribbing, and only the absence of ribbing on the lower portions of the whorl allowed the lines to run their natural course. A clear example of this apparent dependence of the lines on the ribbing may be observed where the lines are more numerous than the ribs and are channeled in the interspaces two by two (Pl. IX, fig. 8): where the ribs end, these lines become unpaired and become all more or less (though very irregularly) equidistant. It may be added that in partly or wholly smooth varieties of these species the lines are generally more irregularly distributed and oriented than in the ribbed varieties.

In some cases, we have a phenomenon which might be termed «secondary correlation». In *Busycon contrarium* Conrad, concentric bands appear at or near the shell surface just proximal to growth breaks (Pl. IX, fig. 10). These bands, which occur only with breaks, may be considered as «subordinate» shell features. The relationship of the shoulder nodes to the breaks is less constant, and might be termed «irregularly correlated»: most often nevertheless, nodes appear at the

level of the growth breaks [51]. The secondary correlation involved is that between bands and nodes: the first will usually cover the last, evidently not because they are directly releated to them, but because both are related to the growth breaks.

VII. Interrelationships between pattern elements

Since the author hopes to be able to give a more extended consideration to that subject in the near future, only a few preliminary remarks will be made here.

The various types of relationship mentioned above as existing between pattern elements and ribbing seem to be present also in the interrelationships between the pattern elements themselves: they are here however often harder to elucidate, owing to the frequent absence of clearly defined «primary» features. Examples of various relationships are given below:

In *Conus generalis* L., when the radial homogeneous bands are well developed, they appear to be quite independent of the transverse sinuous lines.

Presence of «necessarily subordinate» elements is demonstrated by the relationship between cells and frame in networks; more typical cases of subordinate relationship could not be detected anywhere with absolute certainty; and indeed in the usual absence of clearly defined primary elements in shell patterns, such subordinate elements must be rare indeed.

In *Smaragdia viridis* L., black sinuous transverse lines are generally followed by rows of white blotches, often in a very conformable manner (Pl. IX, fig. 9). Yet each of these types of elements may be absent from one to many periodic cycles without the other being noticeably modified thereby. We have thus here to all evidence an associated type of relationship between black lines and white blotches; on account of the variable appearance of the elements, it might be termed an «irregular association». To note, however, that though the author has examined many shells of that species that showed only blotches (esp. in the Caribbean variety *viridimaris* Maury), he has never yet observed a shell with lines only: this, plus the very peculiar configuration of the black lines half-surrounding the white blotches, gives the impression that the latter may be the dominant factor in the colour pattern.

A somewhat similar relationship between elements seems to obtain in the case of some «junction figures». In the complex pattern figures of *Bulimulus coturnix* Sowb., *Neopetraeus arboriferus* Pil., etc. (Pl. V, figs. 9, 10) the relationship of the various parts to each other is always the same, even though the figures

[51] The periodicity of appearance of labra is very irregular, that of the modes much less so. When appearance of a new labrum is very much delayed, a node may be secreted before this new labrum appears, in addition to or in place of the adlabral node; or this interlabral node may continue to be secreted until this labrum finally appears, forming a very elongate node indeed! — see Pl. IX, fig. 10.

are repeated periodically: this to the extent that when owing to a very variable periodicity, the width of periodic secretion is in some places less than the width of the junction figures, these latter will overlap on each other (Pl. V, fig. 9, at right) and still be mostly unmodified thereby. The one alteration that may take place is an elimination, more or less complete, of the overlapping portions of the figures, this especially in *B. coturnix:* but in that case the residual portions of the figures remain absolutely unchanged. The associated relationship of the components of these junction figures is made even clearer in the case of *B. coturnix* Sowb. where in the upper whorls the transverse component may be absent from these patterns: in such a case, the other components will maintain exactly the same position in respect to each other, as if the transverse component were present [52].

It has been indicated above that the juvenile *Neritina communis* Quoy has a homogeneously striped pattern that is later limited to radial bands (Pl. IX, fig. 1): With the original pattern thus split, it is observed that the stripes do not correspond from one band to another: if the unified pattern is restored, then the bands become again continuous across the whorl. We have a similar situation in *Conus generalis* L., where the transverse lines are often discontinuous on each side of the radial bands (Pl. II, fig. 7), but continuous where the latter disappear. This «dissociation» phenomenon is of quite generalized occurence for transverse and oblique pattern elements transected by radial ones (see p. 12). This all seems to indicate that in such cases there is a «general factor» producing an approximately similar periodical secretion for the whole width of the whorl, and an «organizing» factor that will correlate the activities of all the sources in a much closer manner [53]. When the pattern is interrupted, so is the activity of the organizing factor: either this organizing activity is then totally eliminated, or more likely, it acts separately on each isolated region and is uncoordinated over the mantle margin as a whole. – In the case of rib-pattern elements relationships of the correlated type, the ribbing may act as an additional «influencing» factor superposed to or perhaps even replacing the «organizing factor».

[52] A weird feature of this species (or at least of the two specimens at hand) is that the «trees» are interrupted along a radial band that runs at the upper end of the whorl base. Below this band, the stems and leaves have a reverse orientation!

[53] In the rib-denticle relationship mentioned in the author's last work the rib is evidently the «organizing» element: so are apparently the varices of many Gasteropoda for those of the whorl beneath. For ex. in *Scala scalaris,* the varices correspond from one whorl to the next when those of the whorl above impinge, or come close to impinging on the whorl below. As soon as the whorls separate, the varices of the different whorls tend to loose all trace of correlation.

Abstract

The author has endeavoured to give an idea of some of the main types of shell colour patterns to be found in the Mollusca. These are examined, as far as can be done from observations on specimens in a Collection, from various angles: secretion, geometry, ontogeny, relation to sculpture, etc. . . . Among the conclusions drawn from this study, some of the most significant appear to be that: (1) Similar patterns and pattern elements may have very different origins. (2) Juvenile patterns, or portions thereof, may continue to be secreted in the later shell growth stages, even though a very different adult pattern may also have appeared. (3) Truly irregular patterns are almost as rare as truly regular ones. (4) A surprisingly wide range of polygonic figures, often relatively regular, are present in the colour patterns of various Gasteropoda. (5) The relation of colour patterns and elements thereof to ribbing is extremely variable, and may be of at least four distinct sorts.

Zusammenfassung

Der Autor untersucht einige der wichtigsten Farbmuster von Molluskenschalen. Verschiedene Gesichtspunkte werden dabei berücksichtigt (soweit dies an reinem Sammlungsmaterial möglich ist): Sekretion, Geometrie, Ontogenie, Beziehung zur Schalenskulptur usw. Von den Schlußfolgerungen sind die wichtigsten:

1. Gleiche Muster und ihre Elemente können auf verschiedene Weise entstehen.
2. Vollkommen unregelmäßige Muster sind fast ebenso selten wie vollkommen regelmäßige.
3. Eine überraschende Mannigfaltigkeit von polygonen Figuren, von denen viele relativ regelmäßig sind, treten auf in den Farbmustern der Gastropoden.
4. Jugendliche Muster können in den spätern Wachstumsstadien der Schale weiter ausgeschieden werden, auch wenn ein ganz andersartiges adultes Muster in Erscheinung zu treten beginnt.
5. Die Beziehung von Farbmustern und ihrer Elemente zur Schalenskulptur ist sehr veränderlich; es gibt mindestens vier Typen.

Bibliography

BÖGGILD, O. B. (1930): Shell structure of the Mollusks. Mém. Acad. Roy. Sci. Lettres Danemark, Copenhague. Ser. 9, T. 11, n° 2.

COMFORT, A (1964): Molluscan Shell Patterns. — Animals, Vol. 5, n° 5.

COX, L. R. (1955): Gastropod descriptive terminology. Proc. Malac. Soc. London, Vol. 31.

DAVIES, M. (1935): Tertiary Faunas, Vol. I.

NEUMANN, D. (1959): Variabilität der Farbmuster aus der Schale von Theodoxus fluviatilis L.—Z. Morph. Okol. Tiere, 48.

OBERLING, J. J. (1960—1962): Notes morphologiques sur des coquillages. Ann. Mus. Hist. Nat. Berne.

PORTMANN, A.: Animal Forms and Patterns. Publ. Faber & Faber.

ROBERTS, M. (1851): Popular history of the Mollusca.

WRIGLEY, A. (1947): The colour Patterns and Sculpture of Molluscan Shells. Proc. Malac. Soc. London, Vol. 27.

Explanation of the plates

(All figures diagrammatic, variously magnified; view of shell surface, with aperture to the left unless otherwise indicated; arrows, when present indicate distal direction. Asterisks stand for patterns not seen on actual specimens. Alt. c. bands = alternating colour bands.)

Plate I

Fig. 1 End whorls of gasteropod, showing pattern elements resulting from various types of activities of secretion sources.

Fig. 2 b Oblique band: secretion continuous. When secretion of same is intermittent it appears as in fig. 2 a, not fig. 3.

Fig. 4 Cross section through superficial portion of shell, showing the in-depth secretion of spots; in such species as *Natica millepunctata* Lam.

Fig. 5 Various types of junctions of lines. Vertical parallel lines = growth lines

Figs. 6, 9 Valves of two varieties of a *Lioconcha,* prob. *L. castrensis* Lam., showing diverging patterns.

Fig. 7 Zigzags, which include both diverging and converging portions.

Fig. 8 *Marginella lineata* Mühl., showing «inflowing» pattern.

Fig. 10 Irregular zigzags in *Strombus vittatus* L. Zigzags are AB, CD, EF. Dashed lines = connecting lines.

Fig. 11 Rhombic network produced by two sets of lines of opposite obliquity.

Fig. 12 Zigzags of *Strombus vittatus* L., showing directional instability.

Fig. 13 Two connected zigzags of *Strombus vittatus*. Dashed lines = connecting lines.

Plate II

Fig. 1 *Polymita picta* Born, showing crossing of white radial band and dark concentric line.

Fig. 2 Discontinuous near-radial lines in *Littorina zebra* Don.

Fig. 3 Interrupted transverse bands in *Imbricaria conica* Desh.

Fig. 4 Interrupted lobes in *Conus lucidus* Wood.

Fig. 5 Interrupted lines and bands (thick, black) in the reticulated pattern of *Tricolia tessellata* Phil. Figure should be shifted clockwise ab. 45 °.

Fig. 6 «Influence» of a dark transverse band on an alt. c. band, such as in *Gibbula ardens* v. Salis.

Fig. 7 Interruption and dislocation of transverse lines by radial band in *Conus generalis* L.

Fig. 8 Sinuous lines in *Voluta undulata* Lam., showing bends to be closer on their flanks and, presumably in «compensation», more numerous on their proximal extremities and thicker on their distal extremities.

Fig. 9 Crossings of transverse sinuous lines and radial alt. c. bands in *Monodonta articulata* Lam.

Fig. 10 «Influence» of «latent» radial bands on dotted pattern of *Conus arenatus* Brug.

Fig. 11 Closely set transverse lines, showing «nearness» effect.

Figs. 12, 13 Influence of growth breaks on pattern elements: 12 a: interruption of radial bands. 12 b: pause in secretion of radial band. 13: Sinuous transverse lines becoming concentric and straight on the other side of growth break, then becoming again sinuous. G. B. = growth break.

Plate III

Figs. 1–6 c Simple pattern elements of the linear type (except 2 a and 1a, b).

Figs. 6 d–8 Common pattern types in Gasteropods.

Plate IV

Fig. 1 Various theoretically possible simple spot shapes.

Figs. 2–10 Theoretically possible arrangements of «small» elements. 2. Homogeneously irregular. 3. Clustered irregular. 4. Regular perpendicular. 5. Regular oblique. 6. Unidirectional (radial). 7. Two-directional (radial and transverse). 8. Elements arranged in rows. 9. Elements arranged in bands. 10.Elements arranged in crossing pattern.

Figs. 11–13 Some theoretically possible arrangements of «big elements». 11. Elements parallel to each other. 12. Elements touching each other. 13. Elements crossing each other.

Fig. 14 Some theoretically possible arrangements of small and big elements. a) Elements not touching each other. b) Elements touching each other. c) Elements crossing each other. d) Elements within one another.

Fig. 15 Possible relationships of «big» elements with parallel axes (not mentioned in text except for normal parallel and alternate parallel zigzags).

Fig. 16 Rows of spots in a *Mitra* (here *Mitra papalis* Lam.).

Fig. 17 Production of «blurring» in spot margins through different processes. a—d: cross sections through shell, s = shell surface; figures very schematic. a) Spot thinner at margin. b) Spot lighter at margin. c) Spot secreted at deeper levels at the margin. d) Shell substance more opaque over spot margins.

Fig. 18 *Conus striatus* L., showing junction figures of transverse lines and portions of radial bands.

Fig. 19 a, b: arrangements of «small» elements (lobes and dots), as contrasted to c, arrangement of «big» elements, lobed lines.

Plate V

Fig. 1 Crossed-oblique arrangement of spots, as in *Tricolia pullus,* almost as regular as the «regular oblique» arrangment. Spots are here joined by fine lines forming a regular rhombic network.

Fig. 2 Relatively regular arrangement of spots in radial and transverse directions producing also oblique alignments (along the axes x and x').

Fig. 3 *Conus chaldeus* Röd., showing arrangement of spots.

Fig. 4–7 Showing how alt. c. bands may become differentiated from the rest of the whorl.

Fig. 8 Relationship between light ogives and transverse lobed bands in *Conus textile* L.

Fig. 9 Arborescent «junction figures» of *Neopetraeus arboriferus* Pil., showing overlap of the figures.

Fig. 10 Junction figures of *Bulimulus coturnix* Sowb. DD = transverse element. C = radial elements. A = oblique elements.

Figs. 11–14 Illustrating diverse types of periodicity in secretion of divergent elements. In fig. 14, the elements of fig. 11 continue to be secreted until they meet. – The upper and lower portions of figs. 12 and 13 may be referred to as parts a and b respectively of these figures.

Fig. 15 *Neritina glabrata* Sowb. showing elements with different periodicity in upper and lower portions of the whorl.

Fig. 16 *Neritina oualanensis* Les.: Periodicity of element secretion varies in alternate fashion from upper to lower portion of the whorl.

Plate VI

Linear networks

Fig. 1 Irregular network of the crossed-line type.

Fig. 2 Irregular network of the cellular type.

Fig. 3 Irregularly oriented overlapping rectangular network.

Fig. 4 Rectangular labyrinthic network of the cellular type.

Fig. 5 Rectangular labyrinthic network of the crossed-lines type.

Fig. 6 Overlapping irregular patterns.

Fig. 7 Overlapping irregular rectangular network.

Fig. 8 Rhombic labyrinthic network.

Fig. 9 «Tented» pattern produced from light ogives, as in *Conus aulicus* L.

Fig. 10 «Tented» pattern as in *Oliva porphyria* L. In that species and in most other cases, tents point distally (upper arrow [1]), in rare species proximally (lower arrow [2]). AB and CB will be converging lines in the first case, diverging in the second, etc.

Fig. 11 Association of zigzags and regular rhombic network, as in *Strombus vittatus* L.

Fig. 12 Irregular scaly network.

Fig. 13 Scaly network changing into a rhombic one.

Fig. 14 Theoretical derivation of regular triangular network from rhombic one.

Fig. 15 Derivation of rhombic network from elongate light spots, as in *Theodoxus fluviatilis*. Sketch shows pigment rings around distal end of spots.

Figs. 16–19 Derivation of rhombic and hexagonal networks from expansion of light spots of an ocellated pattern until they adjoin neighbouring spots, variously distributed.

Fig. 20 Hexagonal network in the young *Bulla striata* Brug.

Fig. 22 Hexagonal network derived from the crossing of lines, as in *Littorina meleagris*. AA, BB = set of reclined lines crossing the inclined lines CC and DD.

Fig. 23 Hexagonal network derived from transverse zigzags (AA, BB, etc.) and connecting lines (dotted).

Fig. 21 Theoretical derivation of trapezoidal network from regular hexagonal network.

Plate VII

Figs. 1–6 Theoretically possible but actually unrealized linear networks. Fig. 1 Alternating sinuous curves with connectives; Fig. 4 Parallel sinuous curves with connectives. Figs. 2, 3, 5 Various rectangular patterns. Fig. 6 Overlapping trapezoid network.

Fig. 7 Irregular network of lines and spots.

Fig. 9 Regular network derived from alternately parallel sinuous lines.

Fig. 10 Network derived from sinuous lines at right angle to each other (theoretical).

Figs. 11, 13, 14 Networks derived from lobate lines. Fig. 11: Catenate network, from lobate lines arranged «face to face». Fig. 13 Scaly network, from alternating parallel lobate lines. Fig. 14 From simple parallel lobate lines, with connecting lines.

Figs. 15, 19 «Reverse» networks, with colourless framework. Fig. 15: Rectangular reverse framework. Fig. 19: Hexagonal reverse framework.

Figs. 16–18, 20–22 Checkerboard networks.

Fig. 16 Irregular checkerboard.

Fig. 17 Irregular triangular checkerboard derived from triangles.

Fig. 18 Regular triangular checkerboard and «egg and trapeze» network, both apparently derived from a rhombic network, as in *Littorina meleagris* Pot.

Fig. 20 Rectangular checkerboard formed when grooves traverse an ocellated pattern.

Fig. 21 Rectangular checkerboard formed by closely spaced dislocated oblique bands.

Fig. 22 Rectangular checkerboard formed by big «junction spots» of rhombic pattern.

Plate VIII

Diagrams showing unrolled Molluscan shell, with much proximal-distal shortening, to illustrate variety of pattern ontogeny in various genera.

Plate IX

Figs. 1, 2 Same as in preceding plate. Diagrams of *Neritina communis* Quoy and *Meretrix petechialis* Lam.

Fig. 3 Basal whorls of *Pyramidella maculosa* Lam., showing colour pattern on whorl surface.

Fig. 4 Portion of colourless zigzag of *Columbella fulgurans* Lam. crossing three ribs and showing effect of ribs on zigzag.

Fig. 5 Lobe or ogive with «eye-lash» pattern in *Neritina pulchella* Recl.

Fig. 6 Same pattern as in preceding figure, but associated with warts, as in *Neritina squamosa* Swob. (viewed almost tangentially to surface).

Fig. 7 3 whorls of *Pusia tricolor* Gm. Transverse bands regular when associated with ribs in upper two whorls, irregular where the ribs are absent (last whorl).

Fig. 8 *Rissoa grossa* Mich., showing lineoles regular when between the ribs, irregular further down.

Fig. 9 *Smaragdia viridis* L., showing relation of lines to blotches.

Fig. 10 *Busycon contrarium* Conr., showing relation of shoulder nodes to growth breaks (vertical lines) and concentric bands (dark bands to left of lines).

In the printing, the magnifications of the figures for the next two plates have been increased by $^1/_3$ from those indicated.

Plate X

Fig. 1 *Imbricaria conica* Desh. (X 2), showing dark radial lines curving around extremities of light transverse segments.

Fig. 2 *Conus lucidus* Wood (X 1. 2), showing relationship of radial lines and transverse segments.

Fig. 3 *Charonia tritonis* L. (X 2/3), showing relationship of rather vaguely developed dark transverse bands and lobed radial alternating-colour bands.

Fig. 4 *Monodonta articulata* Lam. (X 2. 5), showing relationship of sinuous transverse lines and radial alternating colour bands.

Fig. 5 *Conus striatus* L. (X 1), showing relationship of transverse irregular lines to the radial rows of spots.

Fig. 6 *Conus imperialis* L. (X 1), showing on the lip the relationship of the inner dark areas to the superficial dark lines.

Fig. 7 *Littorina zigzag* Gm. (X 2), showing crossing of lines of opposite obliquity forming network with parallelogram-shaped cells.

Fig. 8 *Helix aspersa* Müll. (X 1. 5), with irregular network.

Fig. 9 *Strombus vittatus* L. (X 4), showing regular rhombic network.

Fig. 10 *Sunetta meroe* L. (X 2), showing rhombic labyrinthic network (near shell margin).

Fig. 11 *Nitidella ocellata* Gm. (X 5. 5), showing (rather indistinctly!) hexagonal network (at base of whorl) derived from oblique rows of isolated ocelli (on other portions of the whorls).

Plate XI

Fig. 1 *Littorina meleagris* Pot. (X 5), showing hexagonal network (right of specimen) derived from the crossing of lines of opposite obliquity, and (upper left) the lines of one set which are straight where they are not «influenced» by those of the other set.

Fig. 2 *Conus abbas* Hwass (X 3), showing lobate pattern that grades into hexagonal and rhombic networks.

Fig. 3 *Terebra dimidiata* L. (X 2), with «reverse» rectangular network.

Fig. 4 *Neritina piratica* Rus. (X 2. 5), with lobate network derived from adjoining transverse sinuous lines.

Fig. 5 *Conus* cf. *pyramidalis* Maur. (X 2), showing hexagonal network derived from transverse zigzags and connecting lines.

Fig. 6 *Babylonia ambulacra* Sowb. (X 1. 5), with reverse hexagonal network.

Fig. 7 *Neritina glabrata* Sowb. (X 5), showing two sets of lines with widely different periodicity.

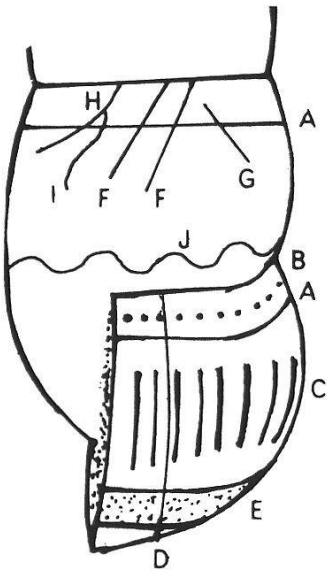
Fig. 8 *Littorina meleagris* Pot. (X 6), showing triangular checkerboard (center of specimen).

Fig. 9 *Oliva porphyria* L. (X 1. 5), showing «tent pattern», and numerous sinuous lines near whorl summit.

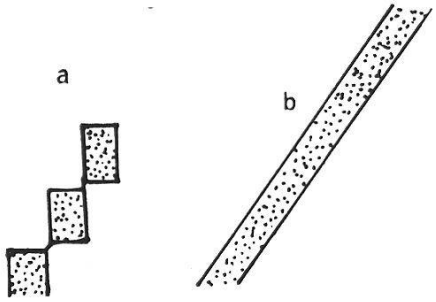
Fig. 10 *Planaxis lineatus* Costa (X 5), showing abrupt change (in middle of penultimate whorl) from a regular «associated» type of pattern to an irregular «correlated» pattern.

Fig. 11 *Pusia tricolor* Gm. (X 9), showing correlated pattern regular when associated to ribs (upper whorl, white transverse bands), becoming completely irregular where ribs are lacking (3 lower whorls).

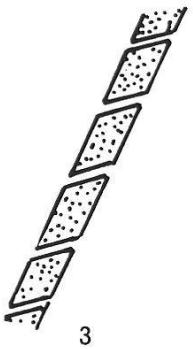
PLATE I



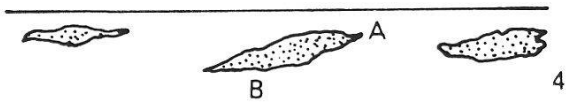
1



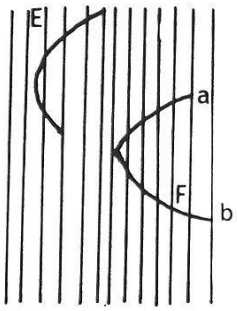
2



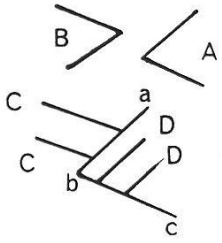
3

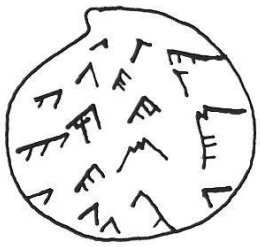


4

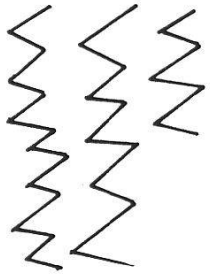


5

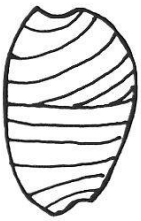




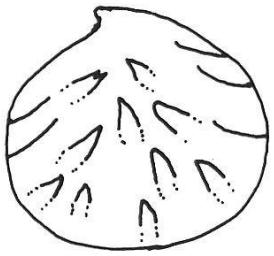
6



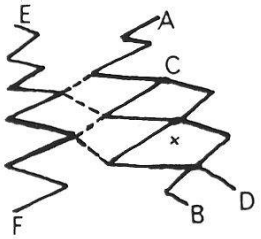
7



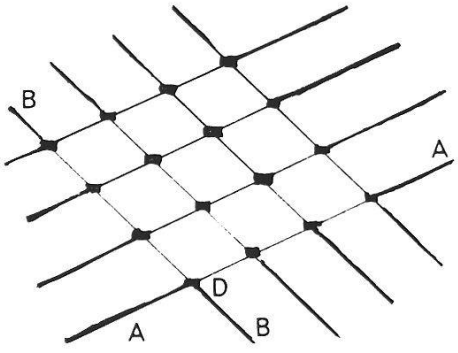
8



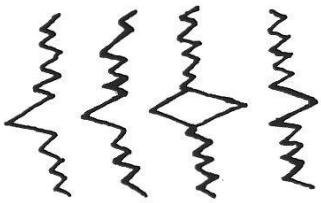
9



10



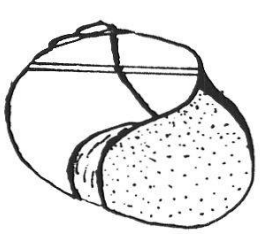
11



12

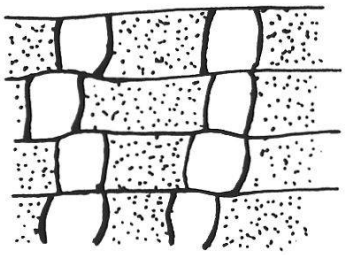
13

PLATE II

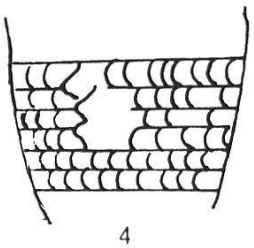


1

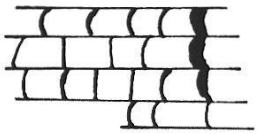
2



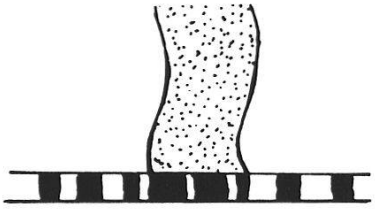
3



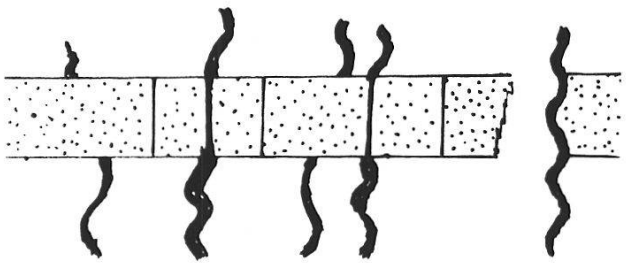
4



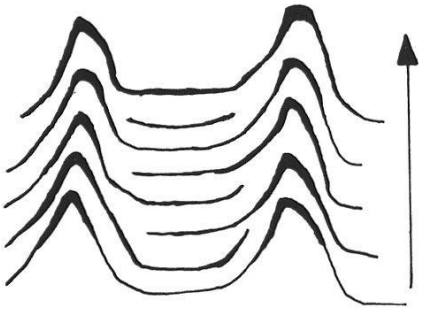
5



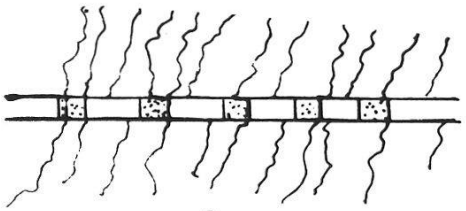
6



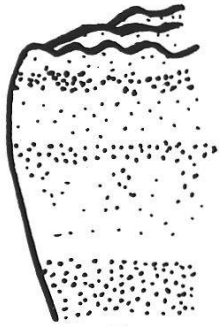
7



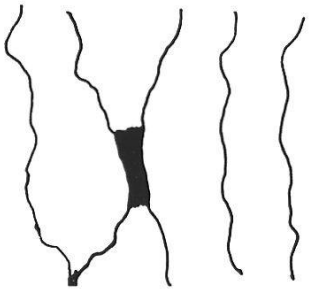
8



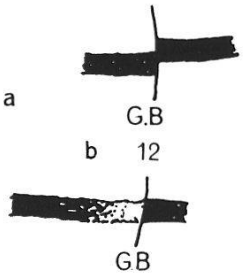
9

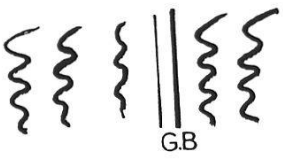


10



11





13

PLATE III

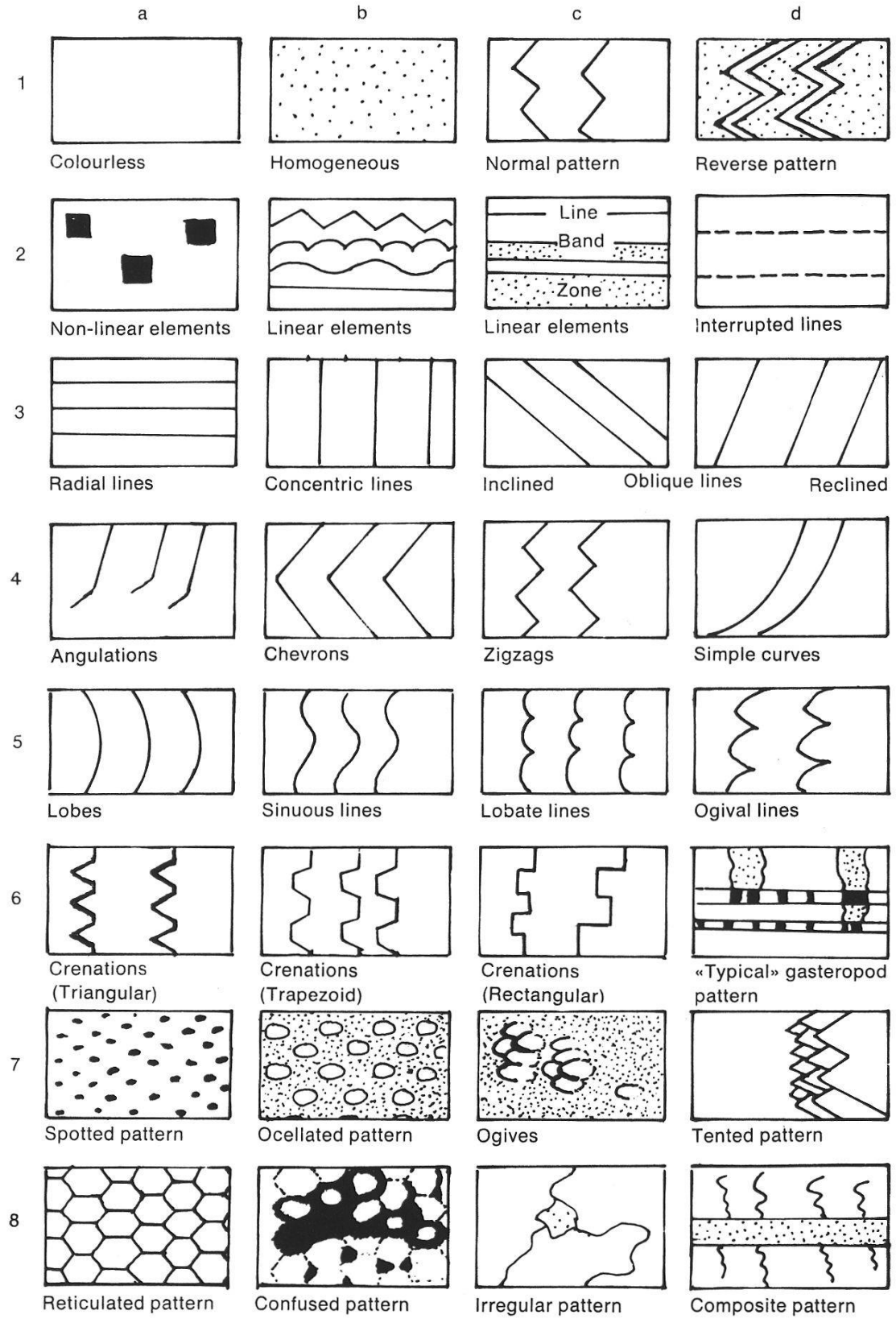
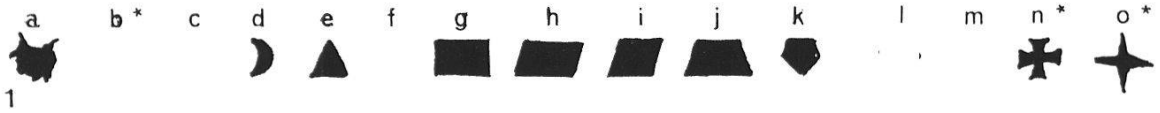
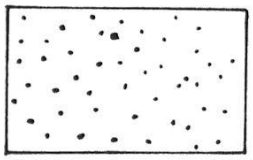

a
b
c
d
1
Colourless
Homogeneous
Normal pattern
Reverse pattern
2
Non-linear elements
Linear elements
Line
Band
Zone
Linear elements
Interrupted lines
3
Radial lines
Concentric lines
Inclined
Oblique lines
Reclined
4
Angulations
Chevrons
Zigzags
Simple curves
5
Lobes
Sinuous lines
Lobate lines
Ogival lines
6
Crenations (Triangular)
Crenations (Trapezoid)
Crenations (Rectangular)
«Typical» gasteropod pattern
7
Spotted pattern
Ocellated pattern
Ogives
Tented pattern
8
Reticulated pattern
Confused pattern
Irregular pattern
Composite pattern

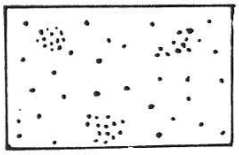
PLATE IV



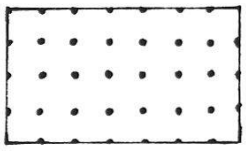
1



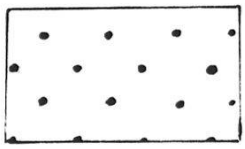
2



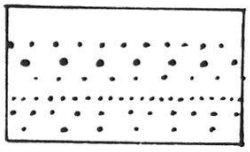
3



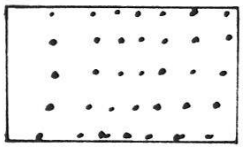
4 *



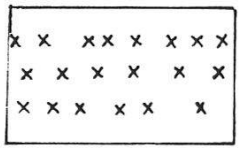
5



6

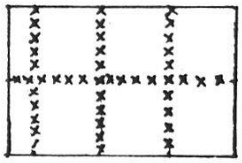


7

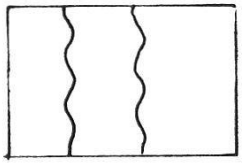


8

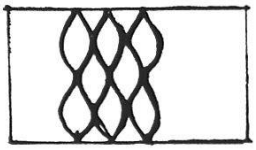
9 *



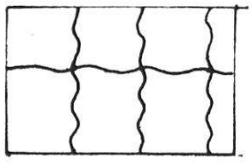
10



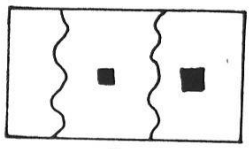
11



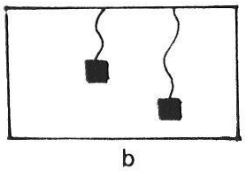
12



13

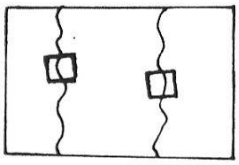


a

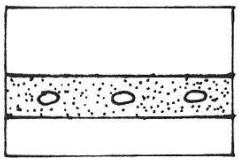


b

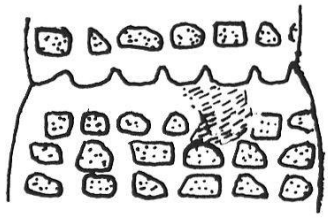
14



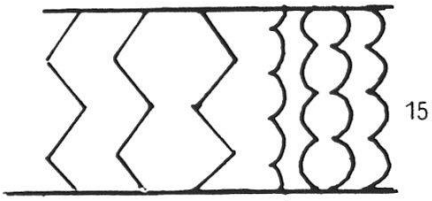
c



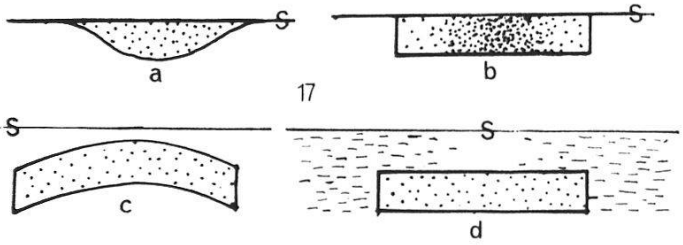
d



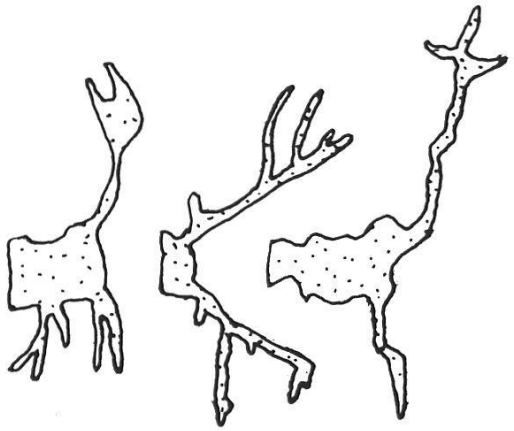
16



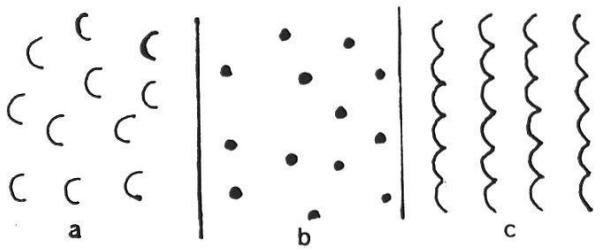
15



17

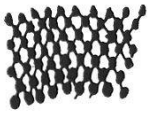


18



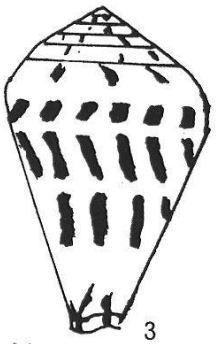
19

PLATE V



1

2

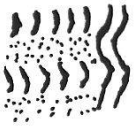


3

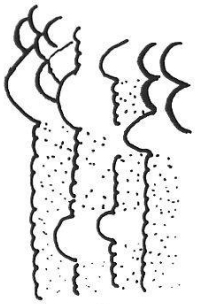
4

5

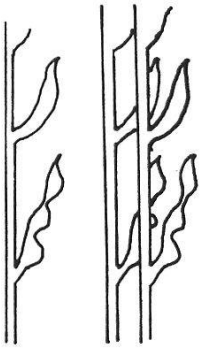
6



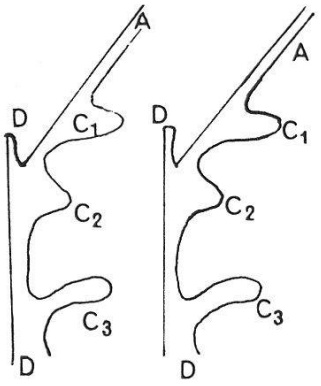
7



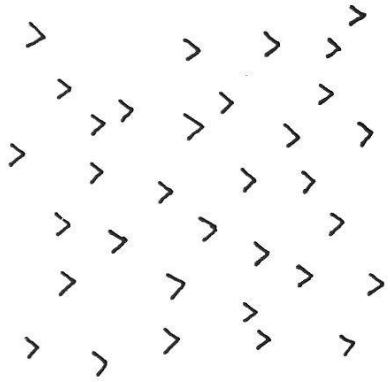
8



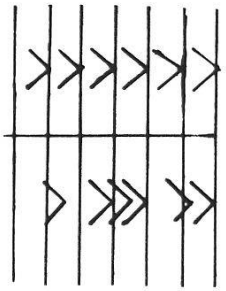
9



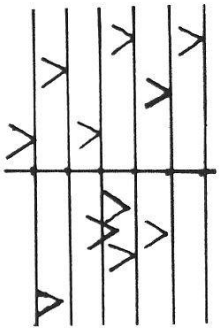
10



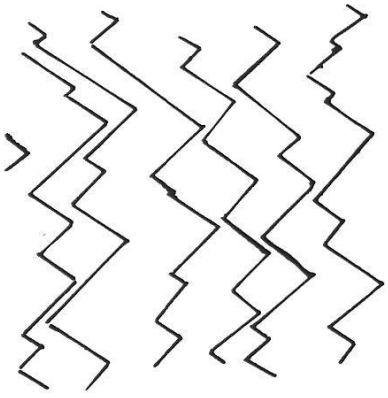
11



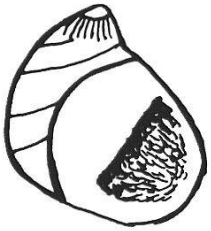
12



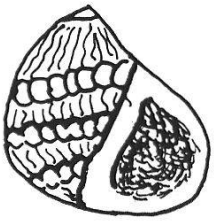
13



14



15



16

PLATE VI

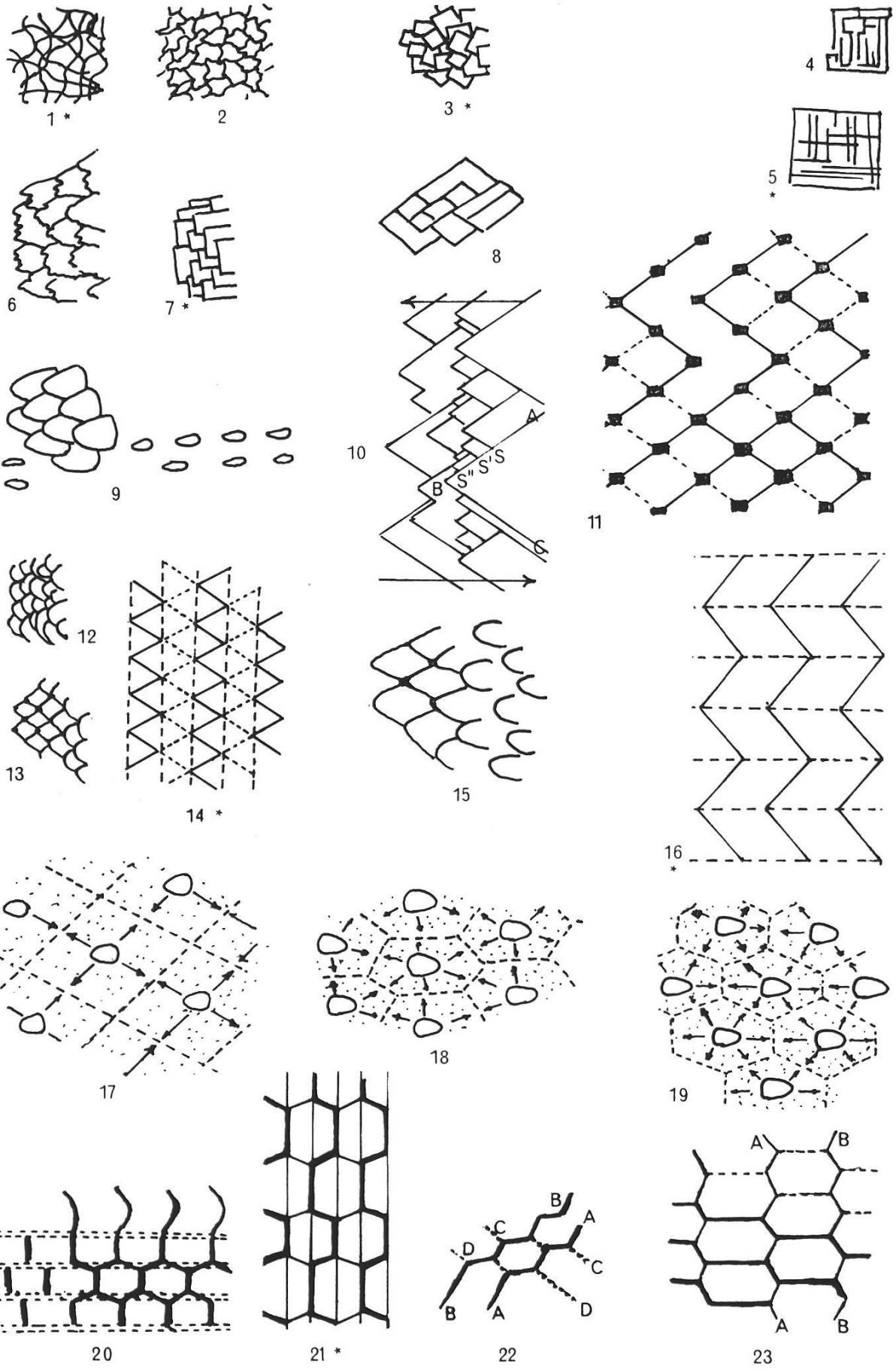
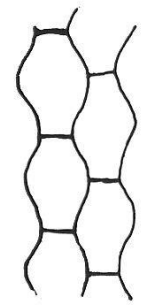
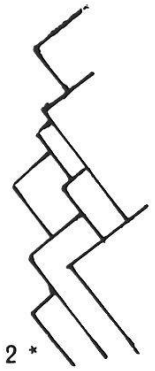

1 *
2
3 *
4
5 *
6
7 *
8
9
10
A
B
S" S'S
C
11
12
13
14 *
15
16 *
17
18
19
20
21 *
22
A
B
C
D
B
A
D
23
A
B
A
B

PLATE VII

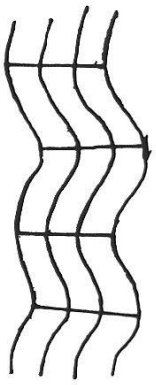


1 *

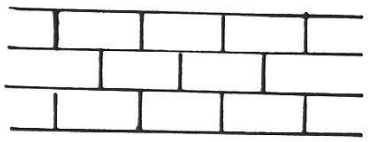


2 *

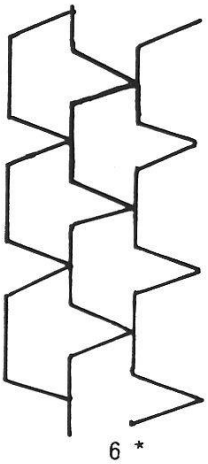
3 *



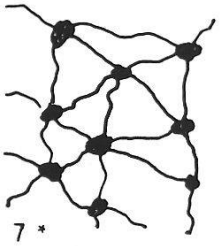
4 *



5 *

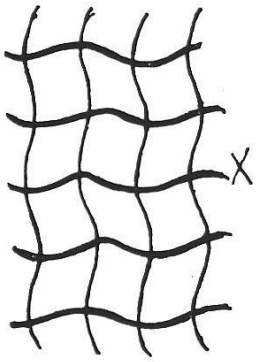


6 *

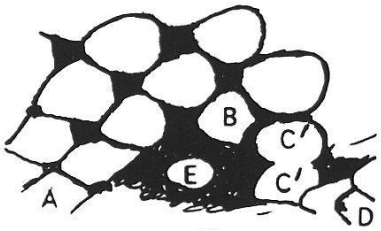


7 *

9



10 *



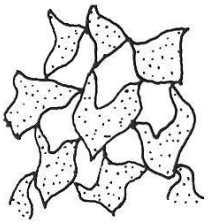
12

13

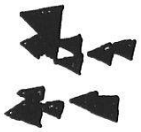
14 *

11 *

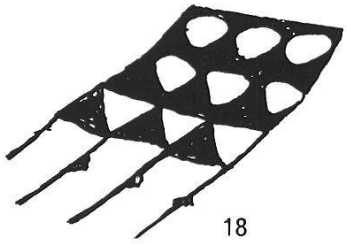
15



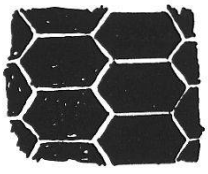
16 *



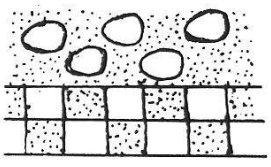
17



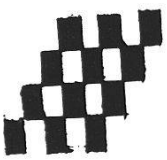
18



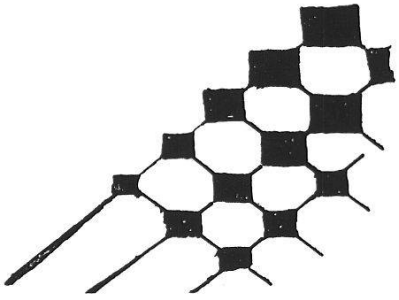
19



20

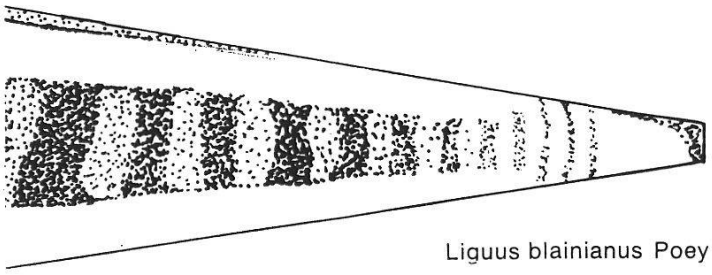


21



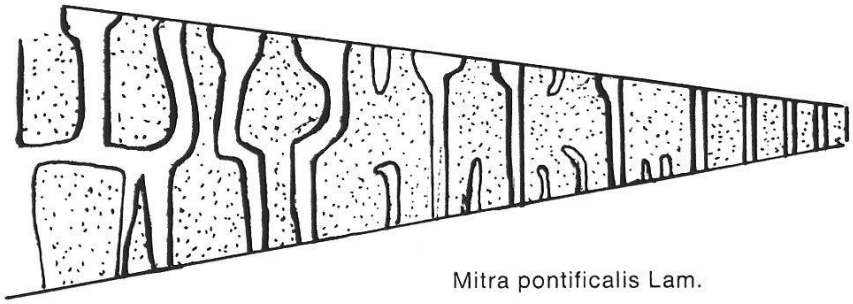
22

PLATE VIII



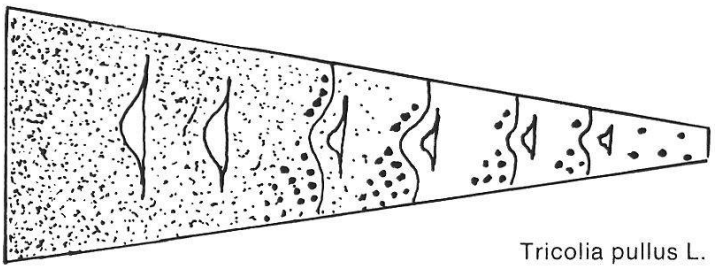
Liguus blainianus Poey

1



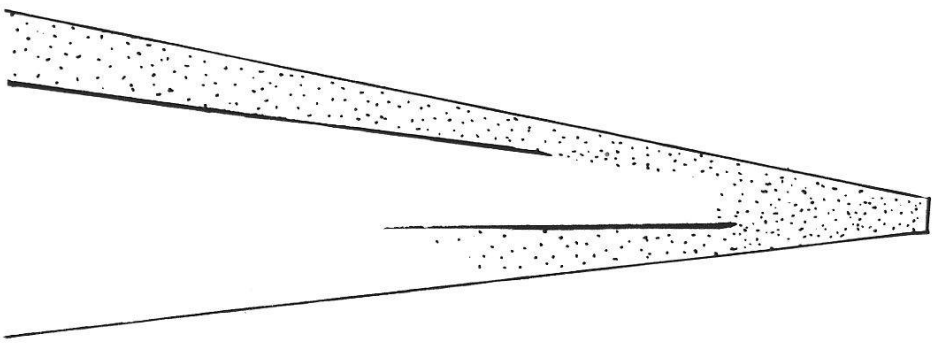
Mitra pontificalis Lam.

2



Tricolia pullus L.

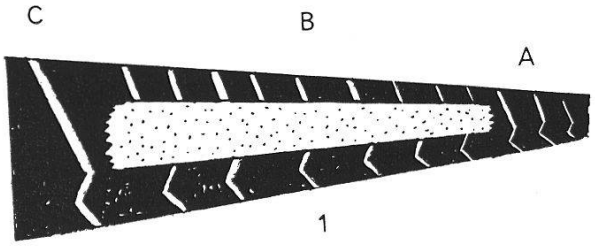
3



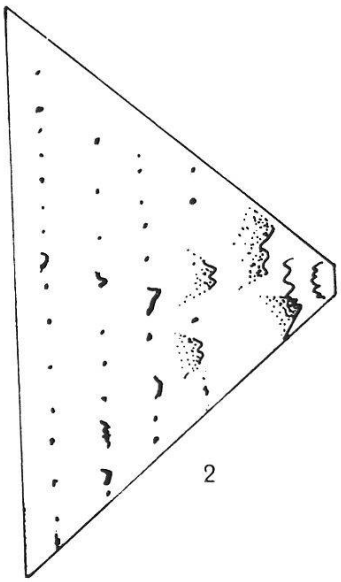
Vexillum vittatum Sowb.

4

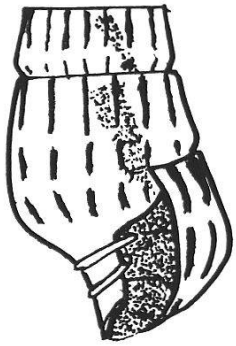
PLATE IX



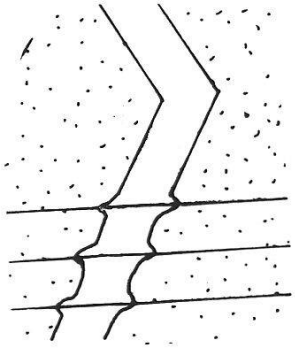
1



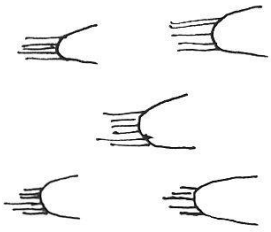
2



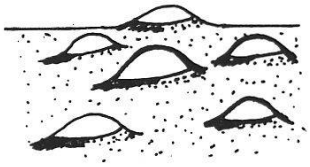
3



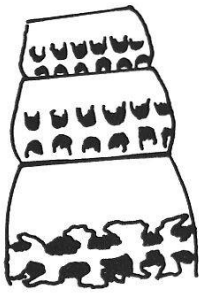
4



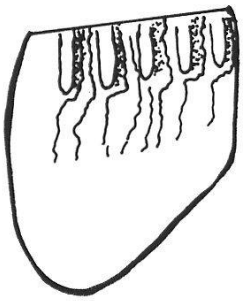
5



6

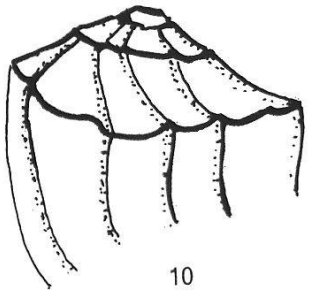


7



8

9



10

PLATE X

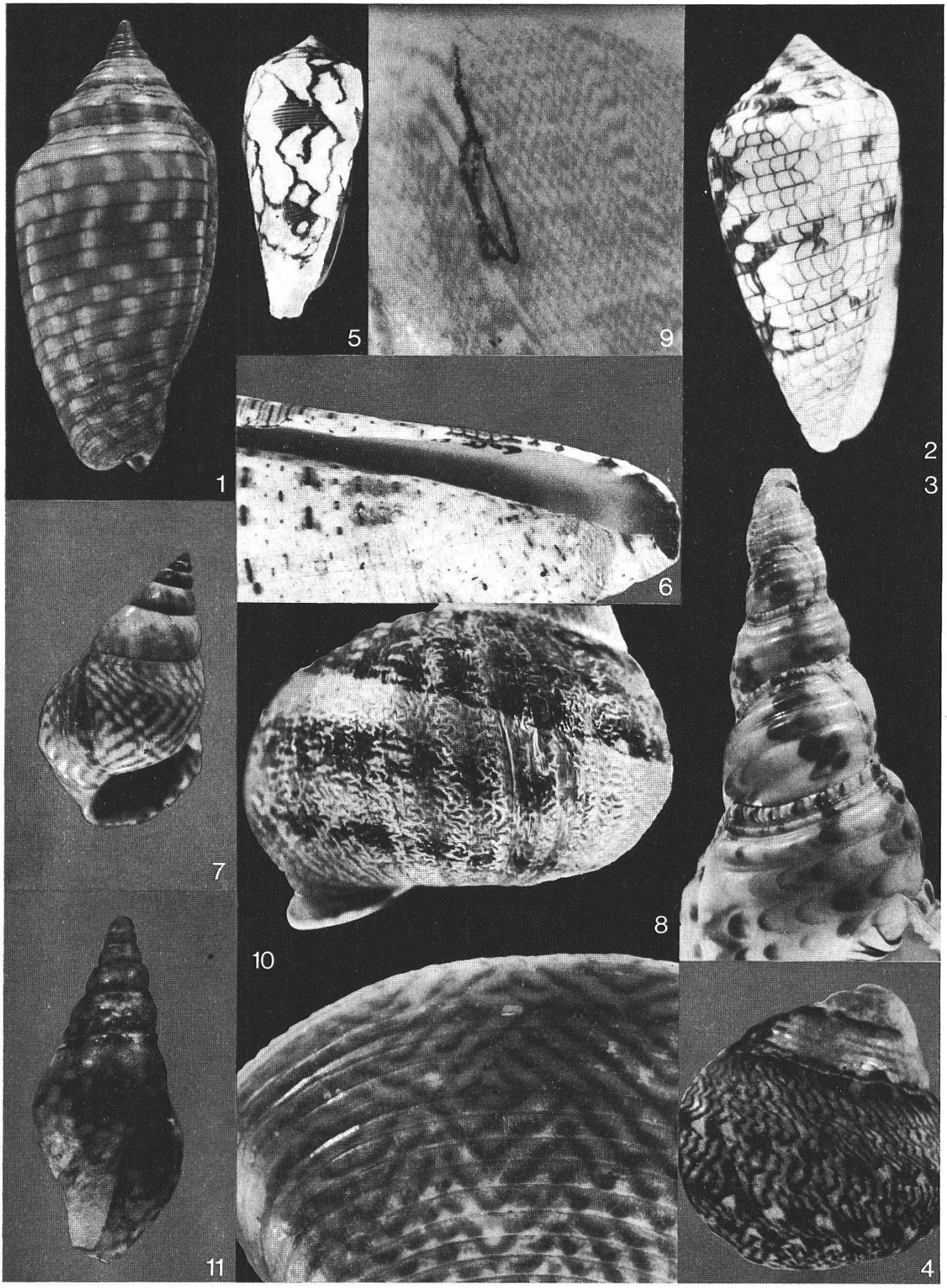
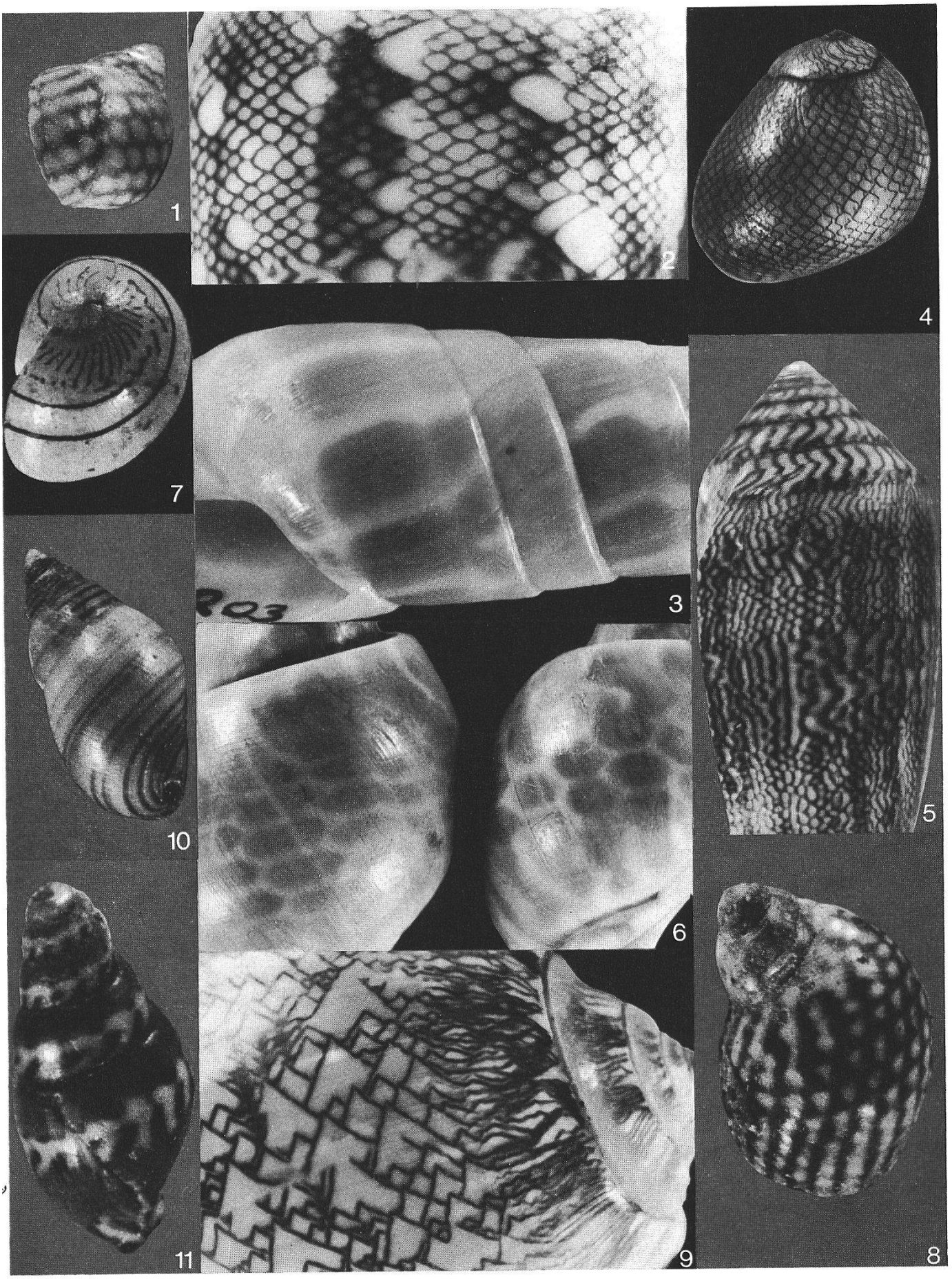



PLATE XI