Geometric classification of possible patterns (produced from a line)

Objekttyp: **Chapter**

Zeitschrift: **Mitteilungen der Naturforschenden Gesellschaft in Bern**

Band (Jahr): **25 (1968)**

PDF erstellt am: **29.05.2024**

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).

R e g u l a r (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 ogiveshaped 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 1½ 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 checker-boards. 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 good-ness» 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 concen-trated 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 pro-cess is not markedly different from (1), from here too secretion otherwise distri-buted 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 checker-boards 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 checker-board 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: