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Color patterns on shells in the Natural History Museum Berne
(abstracted version)

Zusammenfassung

Die vorliegende Arbeit ist im wesentlichen eine Fortsetzung eines im Jahre 1968 in den "Mitteilungen" erschienen Artikels über die Farbmuster von Molluskenschalen aus dem Naturhistorischen Museum von Bern. Während der frühere Artikel die Geometrie der Farbmuster sowie die sekretorischen Veränderungen, die zu ihrer Ausbildung nötig sind, behandelte, konzentriert sich die vorliegende Arbeit auf die Variabilität, die Orientierung und die Abhängigkeit der Musterelemente von Schalenbau und Nachbarmustern. Die ausserordentliche Tendenz dieser Muster zu Zwischenformen macht ihre Analyse extrem schwierig und in gewissem Masse auch subjektiv.

1. Introduction

The present paper is a continuation of our 1968 work in the realm of comparative shell pattern analysis. – As is well known, color patterns of mollusks are composed of one or more components, each made up of a series of elements of similar type and origin, their orientations labeled here as if on the cap-shaped Archetype Mollusk, except for the axial one, not present there. Shell ornamentation is here defined as color pattern plus sculpture. BÖGGILD's terms "inclined" and "reclined" are preferred here to COX's terms "prosocline" and "opisthocline". – The paper will be in telegraphic style, to keep it within manageable dimensions. Owing to space limitations, only the few authors most important for the present study have been cited or listed.

2. Element types (see fig. 1)

a) Linear: Lines, bands, zones etc. . . Streaks, as here defined, vaguely adumbrated linear segments, for ex.: connecting streaks between marginal spots and teeth in *Cypraea arabica* L. . .

b) Non-linear: Dots, specks (less regular in outline, usually white-opaque), spots (normally bigger colored units, rectangular in shape except in *Cypraea*); blotches (more irregular than spots, for ex. in upper whorl parts of *Mitra mitra* L.); areas; clear spots (with or without white-opaque pigment), often distally dark-bordered (except in *Cypraea*), tending to ungulate shape, shield-like when under crossed-oblique influence (ex. *Conus marmoreus* L.) Blurs: normally vague, more or less triangular, fading away from a transverse base often emphasized by "base line", the latter becoming dividing line in the very common blur pairs of contrasting hues (in *Terebellum terebellum* L. light blur distal, dark proximal, reverse of *Nerita polita* L.). Compound blurs, both blur members facing same way (young *Cypraea mauritiana* L.): uncoordinated compound blurs, with members of pair tending to a different orientation type (in *Umbonium vestiarium* L.). Subordinate blurs or blurrings, extending distally from other pattern features (usually from zigzags in Pelecypoda, such as *Glycymeris pectiniformis* Lm., from clear spot borders in prosobranchs, as in many Neritidae). – Blurs dominant non-linear elements in primitive prosobranchs, in chitons, and also in pelecypods, may be ancestral to most other such elements. – Non-linear elements primary, and then either original, or derived (i. e., bordered clear spots from blur pairs in *Nerita polita* by distal curvature of dividing line), or secondary, mere isolated segments of linear elements (spots, as in *Mitra mitra* L.). If blur pairs be the ancestral non-linear elements, then asymmetrical development of light-opaque and colored units (specks and primary clear spots on one hand, dots and secondary spots on other) must have taken place.

3. Orientation of elements (see fig. 1)

Basic pattern orientations related to important shell orientations or (in crossed-oblique), with at least a parallel in other shell features (Chiton microaesthetes, shell microstructures). Orientation grouping here including COX's (1955) "transverse" orientation, comprising both concentric (collabral in spired gastropods) and axial orientations; "free" patterning, or orientations, used essentially in NEUMANN's (1959, p. 410) sense to include all regular rythmic patterning (thus excluding radial and growth-break-related concentric orientations).

a) Concentric orientation. Parallel to growth lines. Main types listed in NEUMANN (p. 265). To note further: gradational banding (as in *Busycon contrarium* Conr.), interrupted gradational banding (in *Muricanthus radix* Gm.), continuous banding (in *Dentalium formosum* Hir.).

b) Axial orientation. Parallel to shell spire axis. Relation to concentric orientation depending on relation of labral profile to shell spire axis (in most Trochidae, profile relatively inclined, axial direction reclined thereto). – Axial subtypes: space-related:[1] constant-distance or parallel infratype (in *Neritina oualanensis* Les., see NEUMANN,

1 "Secretion-rate – related" might be a better term for these elements, see p. 159. If rate indeed involved here, so would (indirectly) time.

p. 354); convergent-divergent infratype (in some Neritina reclivata Say); time-related subtype (top of *Gibbula divaricata* L., see also STRUHSAKER, 1970).

c) Crossed-oblique orientation. Elements oriented in two directions of opposite obliquity. Crossed-oblique lines tending away from periphery to show proximad curling. Same sub- and infratypes as in preceding orientation. May be present:

ca) Fully developed crossed-oblique patterning (rhombic networks, in *Conus mercator* L. band); cb) partially developed one: simple oblique lines, usually reclined but rarely inclined as in *Olivia rufofulgurata* Schep.; whorl-wide chevrons (*Aequipecten latiauratus* Conr.); connected whorl-wide chevrons (*Persicula cingulata* Dlw.); cc) Conflicting crossed-oblique and transverse influences: hexagonal networks (some types mentioned in OBERLING, 1968); cd) Transverse orientation modified by crossed-oblique influence: zigzags. These either stable (all alike), metastable (alike in main outline) or unstable. Stability owed perhaps to radial influence (as in some *Amoria undulata* Lm.), metastable state to influence of preceding zigzag (if located within one zigzag amplitude). Zigzag instability owing either to great inter-zigzag distance (some *Oliva bulbosa* Röd.), or not (true instability, in *Oliva porphyria* L.). – Isolated V's or chevrons apparently mostly portions of zigzags, dissociated for various reasons (in some *Lioconcha,* sides of units sinking in shell and interrupted at bottom of uppermost sublayer, etc.). – Crossed-oblique dot or clear spot arrangments may be nonlinear equivalents of all the above[2], but when homogeneous, presumably equivalent to rhombic networks.

d) Radial orientation. Radial patterning may be homogeneous (light or dark), such banding involving supression, addition to, or replacement of pigment of rest of shell surface; or componential, featuring segments of ordinary free shell patterning (in many Natica); or ground-added, i. e., componential, on a band-distinct homogeneous ground: or component-modifying. Modifications affecting width, number, orientation and color of component segments in bands. Modifications in bands provable only where "normal" patterning present between bands, as in Conus geographus L., with component much wider in bands. Composite bands (with clear center and componential sides) present in some Cones (C. capitaneus L.). Whorl-wide lineation tending to bridge componential bands through the component segments (Monodonta articulata Lmk.), but lineation trajectory unchanged when band sited deeper in shell substance (Amoria canaliculata McC.).

Radial patterning stable where banding constant within species (base band of *Conus virgo* L.), metastable where variability limited and gene-controled *(Cepaea nemoralis),*

2 Or simply outbursts of secretion in alternating spots of mantle margin. Importance of alternation in the production of various crossed oblique patterns not too clear to us.

and unstable where every individual different (and every valve in pelecypods, e. g. many *Tellina*), and variation range unlimited.

e) Radial tendencies

ea) Radialisation: Tendency for a more radial orientation of free patterning. Main types of occurence:
1. Shell surface equally affected (homogeneous radialisation)
2. Switching different in different parts of shell (non-homogeneous radialisation)
3. Radialisation partial (switch usually from transverse or oblique to oblique or hyper-oblique – hyperoblique meaning highly oblique, being often a probable result of some mutation, as in varieties of Conus mercator).
4. Radialisation total (switch usually from oblique or hyperoblique to approximaterly radial).
5. Radialisation gradual. 51 interrupted, 52 uninterrupted
6. Radialisation sudden.
7. Radialisation initial.
8. Radialisation related to depth in shell matter.

Ex.: *Arca zebra L., Dreissena polymorpha* Pal.: (2, 3, 52); *Cypraea diluculum* (2, 3, 7); *Septaria janelli* Recl. (1, 4, 6), pattern alternately radialised and hyperoblique. – Applied to ribbing: *Strigilla carnaria* L. (2, 3, 51). Radialisation, rather than crossed-oblique orientation, dominant factor in production of oblique pelecypod ribbing, probably owing to variety of orientations thus offered to selection. Where switch in pelecypods gradual, it is very rapid and soon interrupted, ribs needing a definite orientation for good functioning (exception: various *Trigonia*).

Peculiar type of gradual, partial and interrupted radialisation (2, 3, 51) apparently owing to temporary loss of orientational control in parallel, space-related transverse lineation (in *Theodoxus danubialis* Zglr. for ex., see also NEUMANN, p. 365). Maintenance of space-related rythm eventually producing a somewhat U-shaped lineation, before control resumption.

eb) Radial desintegration. Transverse elements split into radial lineoles (in some *Nautilus pompilius* L.).

f) (Locally) derived orientations: lobes, etc. . . Festooned lines produced through influence on transverse lines of 1) radial lines, 2) radial ribs. In first case, transverse lines secreted earlier where crossing radial of same hue "like accelerates like", accelerating effect decreasing logarithmically away from line (exception in *Conus boschi* Cl.) – Radial ribs either catalystic or inhibitive, or both (in some *Charonia*, major lineation accelerated, minor delayed in same ribs). – Lines with non-adjoining lobes around specks and clear spots (*Conus textile* L.), as are sinuations. Flammules and lineoles in *Rissoa grossa* Mich. perhaps resulting from irregularities in pigment processing.

g) Irregular orientation. Associated with rugations of same orientation in many Helicidae. Secondarily irregular orientations in lines of *Pusia littoralis* Forb. and some *Nautilus,* probably owing to loss of orientational and rythm control.

h) Orientation combinations: junction figures. These either stable (in *Neopetraeus arboriferus* Plsbr.), repeated without change, behaving as single elements (may overlap with or without partial suppression of latter by earlier figures); or non-stable, in various cones, resulting from secretion-suppression around ordinary element junctions.

4. Structural color patterns

Owing to shell microstructures. Nacreous patterning, the most common, of various types, never on outer shell surface; banding of marginal region of *Cypraea vitellus* L., owing to giant crossed-lamellar units; blue lines of *Patina pellucida* L., produced by light interference on 30°-inclined foliae, the lines lacking the conchiolin that blocks off interference coloring elsewhere, and moreover underlain by deep-seated dark lines setting off blue coloring ever further, as in various Morpho butterflies.

5. Shell ornamentation relationships

Main types of dependant elements defined in 1968 and 1973 articles: subordination (presence of secondary element depending on that of the primary = pattern on *Harpa* varices); association (position of secondary element not modified in absence of primary radial lines in *Planaxis lineatus* Costa); correlation (position of secondary, or other element, or part thereof modified if primary or first element or part thereof absent or weak transverse patterning in many ribbed gastropods). – On the whole, relation between any two ornamentation elements or components showing either:

- Independance (in origin): independance s. s.; independance with influence of one element over other; or with suppression of (part of) one element by another (termed exclusion in our 1973 work): see a, b, bb below.
- Dependance: subordination, association, correlation: see c, d, e, f below.

Term "dependant" used by HENCKE (1948) for vein-spot relationship in butterflies, hopefully covering all ground allocated it here.

a) Influence. Various: physical (substrate on valve of Anomias); concentrational (pigment of zigzags concentrating on ribs of *Arca*); configurational (conformity of spot to tooth shape in various *Cypraea* and of band segments to beads in *Clanculus pharaonis* L.); orientational (pigmented radial bands or radial grooving tending to reduce free elements crossing them to concentric segments); accelerative, decelerative, etc. . .

b) Suppression

ba) Place suppression often involving suppression of parts of linear elements by non-linear elements (ex. *Conus textile*). Suppressing elements usually light, major-component elements; suppressed dark, minor-component lineation. Beyond suppression zone, where effect weaker, may be present a "repulsion zone", deflecting the lines. Specks, such as in *Smaragdia viridis* often surrounded by broad suppression-repulsion zone; in clear spots, zone often limited to spot. Linear suppression is that of radial bands and concentric varices; distad loops in component-modifying radial bands presumably homologizeable to repulsion, in Amoria undulata Lm.

bb) Time repulsion. Suppression of early parts of later elements by distal parts of earlier elements of same type (in many clear spots, in unstable zigzags, as in *Oliva porphyria* L.), sometimes of distal parts of earlier elements by proximal parts of later (in *Terebellum terebellum*). Absence of suppressive tendencies leading to mingled zigzags (in *Oliva mustellina* Lm.) and other oddities.

c, d) Association and subordination with great variety of types.

e) Correlation involving at various times: transverse lines with ribbing; portions of transverse lines in relation to each other; varices of one whorl with those of whorl above; columellar teeth with fasciolar folds; marginal denticles with external ribs in some pelecypods. In all cases, dissociated position between correlated elements possible through loss of contact between these – or through weakening of one of the partners, especially the primary partner, where present (ex. weakening and vanishing of ribs in adult of *Pusia littoralis* Forb. leading to aberrant behaviour of correlated white lines) – also to rythmic uncertainty during switch from one rythm to another, as in color elements of young *Clanculus pharaonis* L. May also have permanent dissociation, where, as in *Marginella adansoni* Kien., average rythm about same for ribbing and lineation, but the last changing gradually from a slower –, to a faster-than-ribbing rythm. May also have positional alteration without true dissociation, through whole-number rythm multiplication of color lineation (as in adult of *Rissoa grossa* Mich., where one line in interspace center replaced by two lines at interspace sides).

f) Dependant characters mostly to all appearance resulting from same genic factors as their primary elements. Subordinate characters: presumably epiphenomena; associated: possibly pleiotropic features. Same may apply to typical (rib-color) correlated characters, the difference with associated being perhaps the more stable orientation or position of associated characters. Occasional rythmic divergence of coloring with ribbing indicating, in correlated characters, presence of additional factors affecting coloration, not ribbing: while in varix-varix correlation and in single transverse elements, dissociation proving that various factors (probably non-genic) in addition to the frequency factor, contribute to the location of any one element. In columellar teeth-fasciolar fold relation, suggestion of two factors, with selective action on columellar teeth-producing factor.

6. *Other pattern phenomena*

a) Reduction and drowning. Presence of two transverse components even in primitive gastropods implying a pattern reduction in case of one-component or patternless taxa. Pattern reduction actually observable in many species (*Smaragdia viridis L., Conus testudinarius* L.). Pattern "drowning" on other hand resulting from influx of additional pigmentation. Seen in *Neritina virginea* L., where affecting background, and in *Lioconcha castrensis* Lm. the elements, in both cases merely an expansion of already dark areas or features. In some *Bulla striata* Brug., etc. . . pigment blotches added to original pattern.

b) Twinned and paired elements. The first derived apparently either from line splitting or rythm multiplication: seen in various *Gibbula.* Paired features: closely spaced blurs and dots of contrasting shade.

7. *Patterns in sections*

Shell layer names here much as in OBERLING, 1979. Ectostracum, diostracum, hypostracum from outside in. Ectostracum often divided in upper and lower sublayers with further occasional divisions thereof. Color (pattern) layers here referred to as color (pattern) strata. Pattern strata termed thick, rather thick, or thin according to (sub)layer portion they occupy (ex. *Conus chaldeus* Röd. pattern stratum thick as encompassing all or almost all upper sublayer thickness). Thin strata usually found at sublayer boundaries (as in lower stratum of *Oliva porphyria*).

Pattern rarely limited to periostracum (*Mitra zonata* Mar.), but usually to ectostracum, and indeed to outer sublayer thereof where present; though in various species major component residing in upper portion of lower sublayer (ex. *Fasciolaria hunteria* Pèr.), or even further down (in *Conus lividus* at diectostracal boundary, impinging on both layers). In some shells (esp. olives, but also some cones, such as *C. terminus* Lm., and some *Lioconcha*) complete patterns appearing at two levels in the shell wall; in some olives, owing perhaps to reflected marginal region and presence of fast-growth opaque division at periphery (= lower limit of upper sublayer) that appears to bisect pattern stratum there located, formation of three superposed shell patterns (upper, lower, lowermost). In some, elements actually bisected, two portions thereof appearing, owing to marginal convexity, as mirror images of each other (*Oliva tricolor,* fig. 2). In others *(O. porphyria),* elements in strata on both sides of opaque division apparently unrelated. In *Cypraea* likewise, three patterns occasionally lying one below the other: but here lowermost pattern is normal ectostracal pattern, above patterns secreted in two sublayers, dorsal and marginal (especially dorsal extension thereof), secreted thereon after end of shell growth.

Frequent expansion of pigment area along slow-growth laminae. Apart from features basically independant of such laminae but with expansions thereat (many dots in *Conus arenatus* Hw., for ex.), other features "laminae-related", limited to one or a group thereof: or laminae-bounded (usually distally), both in many olives. This phenomenon manifesting itself on the "micro" scale, even in essentially non-concentric elements.

Sections helpful in understanding of three-dimensionality of elements. For ex. non-linear elements often spheroids: dots of *Conus arenatus,* clear spots of *Pyrene pardalina* Lm., and of *Conus marmoreus* – in the latter species only upper part of spheroid observed as ground color very shallow, and white of spot fusing below it with general white of shell. Specks on other hand, especially those in *Cypraea testudinaria* L., highly irregular, grain-like, or shaped like icebergs or mountainous islands, and when affected by laminae-related expansions, ressembling cone-in-cone structures, mushrooms or even atomic clouds.

Shell surface phenomena also obtainable in sections: for ex. "like precipitates like", in *Conus chaldeus*, where lower color stratum secreted earlier when underlying upper pattern elements, see fig. 2.7 (secretion of elements at depth proceeding directly downward like microstructural elements, and for same reasons, see OBERLING, 1979); in *Oliva porphyria,* repulsion, toward the surface, of lower stratum transverse lineation, at level of clear radial band of that pattern. – Irregular correlation between elements from lower and upper patterns in *Conus gubernator* Hw.

8. Coloration-ribbing relationship

LINDEN (1896, p. 313) presupposed inverse relation between pigmentation and shell secretion rate, with later increasing in ribs (p. 307), and WRIGLEY (1948) asserted radial ribs to be light, depressions dark. – As seen by us, light coloration of raised features often present where ground color concerned. Dark depressed features especially prominent where callus secreted on earlier-produced sculptured surfaces, as parietal region of *Harpa,* or dorsal surface of various *Cypraea,* particularly of *C. isabella* L., with deposits there often showing Liesegang-like phenomenon. – Light coloration on transverse ribs in most occasions, except in presence of coarse units of major transverse component, at times rib-borne (in many Fusinidae): and growth-break features, these tending to be pigmented even where raised *(Muricanthus radix).* In radial direction linear elements tending to coincide with narrow ribbing elements, whether grooves (*Planaxis lineatus* da Costa) or ribs (various *Ficus*): and free patterning pigment tending most often to concentrate on radial ribs, leading to darker ribs when ground color absent (*Tonna tessellata* Lm.). – Conformity between patterning and sculpture (affirmed by WRIGLEY, 1948) true in various fashion (see above chapters). Generally not true for radial bands, usually broader than any ribbing.

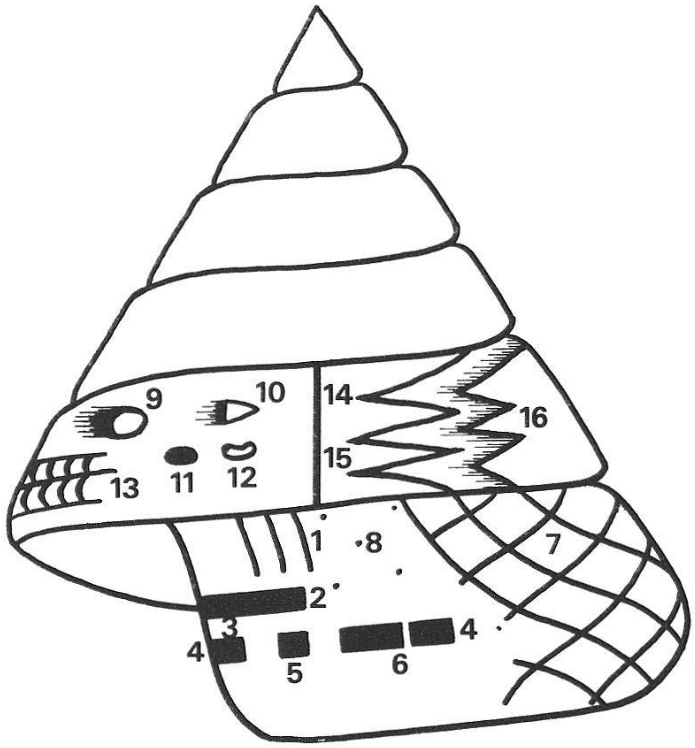
9. Components

WRIGLEY's (p. 212) major and minor free components valid at least for prosobranchs: other mollusks rarely with two such components on single shell. Two components unrelated in virtually all respects. For ex., in major components (this applying also to radial bands), elements, when of same hue as component, are favored as regards size and/or frequency[3], in minor component merely aligned. Components either simple or composite, with sometimes complex system of elements and intervals, as in some *Smaragdia viridis*. In some prosobranchs more than two components present: maximum count in *Voluta musica* L., with at times 3 free and one rib-subordinated component. – Each component presumably produced by independent (genic) factor: other factors no doubt responsible for radial patterning. At least another factor, moreover, regulating phase changes during shell growth (see WANSCHER, 1971). –

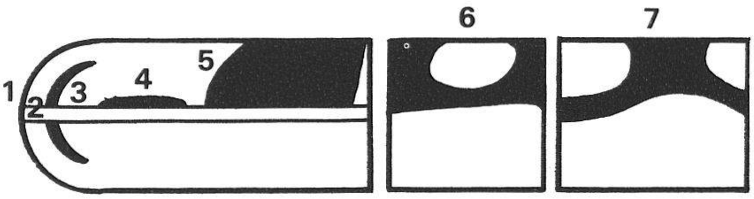
Time involved in various ways in free element secretion: directly in time-related patterning (see p. 153); perhaps indirectly in "space-related" one (see below). Minor radial patterning, and spots in *Cypraea* as well, reflecting presence of some space rythm or frequency factor. – Factors appearing to act in diverse fashions: rythm control of unstable zigzags evidently acting on feature starts, with proximal-distal element amplitude determined by other factors, not necessarily genic: the reverse in overlap junction figures, with evident genic figure[4] control and other-factored rythm. Direct factor control in irregular non-linear patterning (e. g., in *Conus ammiralis* L.) evidently limited to element type determination, and in various *Conus* and *Cypraea* also to that of element frequency, but not to secretion of any single element. In "space-related" lineation (parallel lines, etc.) rythm control seemingly from one element to the next, perhaps through steady pigment (precursor) inflow, in a system of alternate pigment (precursor) build-up and dissipation, either through the WADDINGTON and COWE (1969) system or through one of pigment accumulation-cum-inhibition, and subsequent pigment release, either total or partial, beyond a certain threshold. Various modifications of either system (for ex. with only pigment above threshold released) needed to explain zones around specks. Possible combinations and intergrades between all these theoretical pattern-producing methods, and others as well, almost as numerous as actual intergrades between various pattern elements.

3 Example in *Conus arenatus* Hw., etc. . .

4 The figure control would itself involve time, if only indirectly.



1. Shell surface.
1. Concentric lines. 2. Radial additive band. 3. Normal surface band. 4. Radial band, which at 5. is componential, to the right at 6. component-modifying (w. element expansion). 7. Crossed-oblique network, becoming a crossed-oblique dotted pattern to left (8). 9. Clear spot with distal border and dependant blurring. 10. Paired blurs with median dividing line (thickness of this and of distal border of spot. 9. much exaggerated). 11. Dot. 12. Speck. 13. Radial lines with lobes. 14. Axial line. 16. Zigzag with subordinate blurring. 15. partially radialized zigzag.



2. Shell section.
Left: section of an Oliva, with 1. convex marginal region and 2. opaque central division at base of upper sublayer of ectostracum. 3, 5. Laminae-related and laminae-bounded color elements, both thick in the up-down direction in contrast to the thin stratum at 4.–6. Middle section showing clear spot in dark ground. Right section: Horizontal stratum secreted earlier when under surface element (7), and fusing with its base.

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