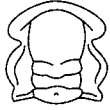


The colour patterns of cypraeid gastropods

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Colour patterns on mollusc shells are usually controlled by one-dimensional morphogenetic programmes. In adult cypraeids, by comparison, colour patterns are two-dimensional in morphogenesis and three-dimensional in structure. Visible patterns usually result from the uneven thickness of a pigmented layer, rather than from a spatially uneven concentration of pigment. Specialized sculptures in a few cypraeids may be regarded as extreme examples of three-dimensional colour patterns. Morphogenesis of some patterns is controlled by three-dimensional relief of the underlying shell surface. Computer models successfully reproduce key characteristics of cypraeid colour patterns. Since most cypraeids possess colour patterns, while few of the combinations of factors controlling these programmes yield a pattern, these patterns can be expected to have a yet undemonstrated adaptive value. □ *Shell colour, shell sculpture, morphogenesis, self-organization, computer modelling, Gastropoda, Cypraeacea, Cypraeidae.*

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Cypraeid gastropods display a terminal, or determinate, growth pattern (cf. Vermeij & Signor 1992), which is a mode of growth characterized by the shell attaining a final size and thereafter ceasing to grow (except for secondary changes in shell thickness and apertural characters). Terminal growth in this family is rendered obvious by distinctive morphologic characters that mark the attainment of final size.

Colour patterns on juvenile cypraeid shells often consist of spiral or divaricate bands, which are characteristic of shells that grow by marginal accretion (e.g., the detailed analyses by Meinhardt 1984, 1995a; Meinhardt & Klingner 1987; Gunji *et al.* 1993). These patterns are the result of one-dimensional morphogenetic programmes. Since shell growth records the activity of this programme in time, the resulting pattern can be regarded as a two-dimensional graph. The colour patterns on the dorsal region of adult cypraeid shells, by contrast, often consist of round or irregular patches, rings, or a complex meshwork (e.g., Figs. 1A, D, 2–4). These patterns are unlike any generated by one-dimensional programmes.

The cause of this striking difference is that adult patterns are secreted on top of a pre-existing region of shell by the two-dimensional epithelium of a mantle lobe. Unlike the condition in shells which grow by marginal accretion, the mantle surface remains stationary with respect to the shell. Meinhardt (1989, 1995a, b) and Kondo & Asai (1995) used computer modelling to illus-

trate the results of two-dimensional morphogenetic programmes that generate self-organizing patterns of patches and/or stripes. These models are based on a reaction–diffusion system involving an activating and an inhibiting morphogen (see also below).

The present paper concentrates on the morphology of a few patch and/or stripe patterns in adult Cypraeidae, and analyses indirect evidence on morphogenesis obtained from the morphology of these patterns, of the underlying shell surface, and of the facing mantle surfaces.

Material and methods

Living specimens of *Cypraea arabica* Linnaeus, *C. histrio* Gmelin, *C. isabella* Linnaeus, *C. lamarckii* Gray, *C. lynx* Linnaeus, *C. miliaris* Gmelin, *C. tigris* Linnaeus, *C. mauritiana* Linnaeus and *C. vitellus* Linnaeus were collected in the intertidal to shallow-subtidal zone at several localities around the islands of Cebu, Mactan, Hilotongan and Cabuyan, central Philippines, in November 1994. After observation in aquaria, selected specimens were allowed to expand fully, then were anaesthetized with magnesium sulphate, fixed in 5% formalin and subsequently preserved in 5% ethanol.

Several other cypraeid species were collected on the same occasion, but because of the nature of their colour

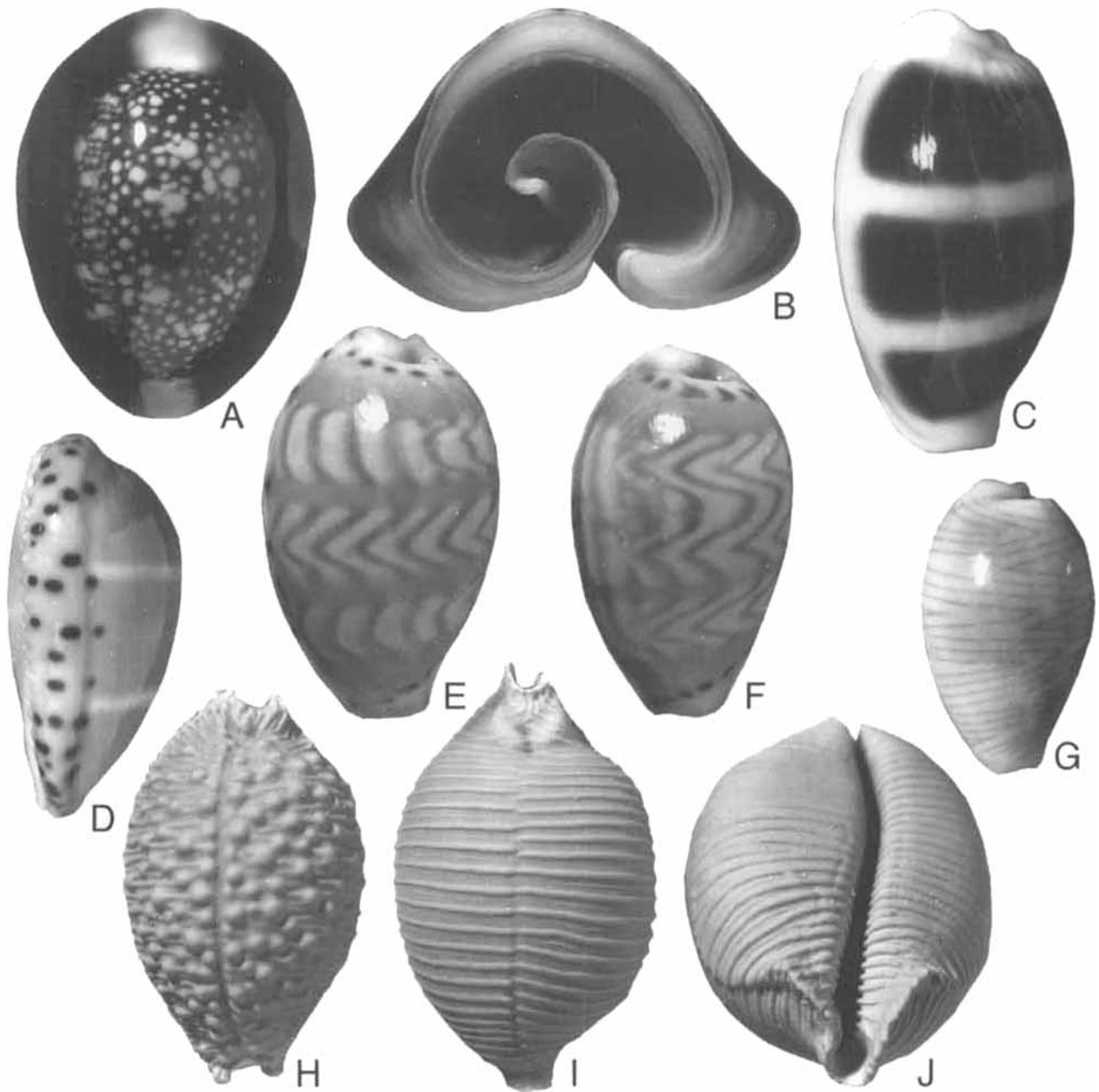
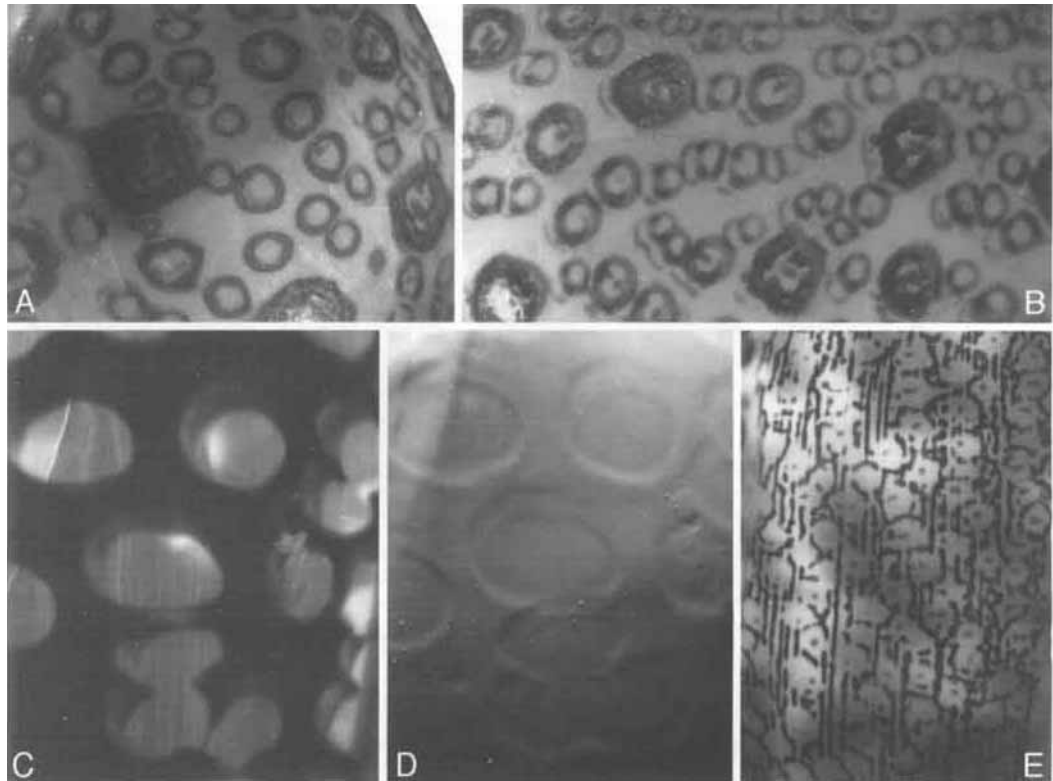


Fig. 1. Recent cypraeids from Cebu Island, Philippines. □A–B. *Cypraea caputserpentis* Linnaeus, $\times 2$ (A) and $\times 3$ (B, cross-section). □C. *C. asellus* Linnaeus, $\times 3$. □D. *C. lutea* Linnaeus, $\times 2.5$. □E–F. *C. ziczac* Linnaeus, $\times 3$. The specimen in □E shows the typical colour pattern, while the divaricate nature of the colour pattern is more clearly visible in □F. □G. *C. clandestina* Linnaeus, $\times 3$. □H. *C. nucleus* Linnaeus (whitened), $\times 2.5$. □I–J. *C. childreni* Gray (whitened), $\times 2$ and $\times 2.5$, respectively.

patterns were not relevant to the present study. Comparison material was provided from the author's collection, from shell shops in the Philippines, and from the collections of the National Museum of Natural History, Smithsonian Institution, Washington DC, USA, and Swedish Museum of Natural History, Stockholm, Sweden. All illustrated material is in the possession of the author.

This paper follows a conservative taxonomic approach and regards all Recent cypraeid species discussed herein as belonging in the genus *Cypraea*. Although several generic and subgeneric taxa have been recognized among these species (e.g., Schilder 1924; Schilder & Schilder 1971), these taxonomic categories are difficult to characterize by non-specialists. In addition, their use in this paper would have been irrelevant to the present discussion.

Fig. 2. Details of colour patterns in Recent cypraeids from Cebu Island, Philippines. □A–B. *C. argus* Linnaeus, $\times 3$. □B shows an instance of ‘double-exposure’ anomaly. □C–D. *C. mauritiana* Linnaeus, $\times 2.5$. Colour pattern (C) and associated relief (D, whitened). □E. *C. histrio* Gmelin, $\times 3$. Anomalous specimen showing pigmented dots at the centre of non-pigmented patches.



Mantle and shell morphology

Juvenile cypraeid shells are thin and possess a broad aperture. Their general aspect is superficially reminiscent of the shell of the opisthobranch *Bulla*. At onset of the adult stage, the outer lip folds inward and develops a row of rounded teeth. Similar teeth are built on a callus growing on the parietal side. The aperture becomes constricted to a narrow slit, at which stage linear shell growth stops.

When the mollusc is fully extended, a mantle fold expands from each side of the aperture and wraps around the shell, completely enveloping it. In the adult, these mantle folds secrete secondary layers of shell material onto the outer shell surface.

In a few Palaeogene cypraeids, extreme specializations were reached in the selective secondary thickening of the outer surface. *Rhynchocypraea* substantially elongated the anterior and posterior canals into rostra. A broad peripheral keel built all around the oral side of the shell by *Pallioocypraea* increased the resting area of the shell on the substrate almost threefold. *Gisortia* and *Vicetia* built two massive transversal keels on the anterior and posterior regions of the dorsal and lateral surfaces. *Gisortia* also built one or a few large tubercles, or thick blunt spines, on the posterior region of the shell (e.g., Cossmann 1903, 1906).

Comparable but less-developed characters occur in Recent cypraeids. For instance, projecting keels (secondarily enveloped by a sculpture of subparallel ridges) are built near the anterior and posterior canals in *Cypraea childreni* (Fig. 1J). Several Recent species of *Cypraea* build a thickened peripheral keel (Fig. 1A–B). *C. marginata* builds a thinner, undulating peripheral keel. *C. martini* and *C. friendii* secondarily elongate both siphons and bend them in the dorsal direction. *C. bistrinotata*, *C. margarita* and, to a lesser extent, *C. cicercula* elongate the sides of both siphons into two pairs of blunt spines.

Shell morphology. – The position where the two mantle lobes meet, the morphology of the contact region and the aspect of the corresponding shell region are specific characters. The contact region of the mantle lobes often corresponds to a distinctly coloured line, band or groove on the shell surface. This feature is called dorsal groove in the taxonomic literature on the Cypraeacea. The term is somewhat misleading, however, since the feature is often not a groove and is usually displaced toward the right side rather than being dorsal. Because of the variable placement and aspect of this character (see also below), it is called *apposition line* in the following discussion.

Sometimes the apposition line corresponds to a clear discontinuity in shell relief and/or pigmentation, caused by differences in pattern and/or intensity of the pigmentation secreted by either lobe (Figs. 1H–I, 3A–B, 4I–L).

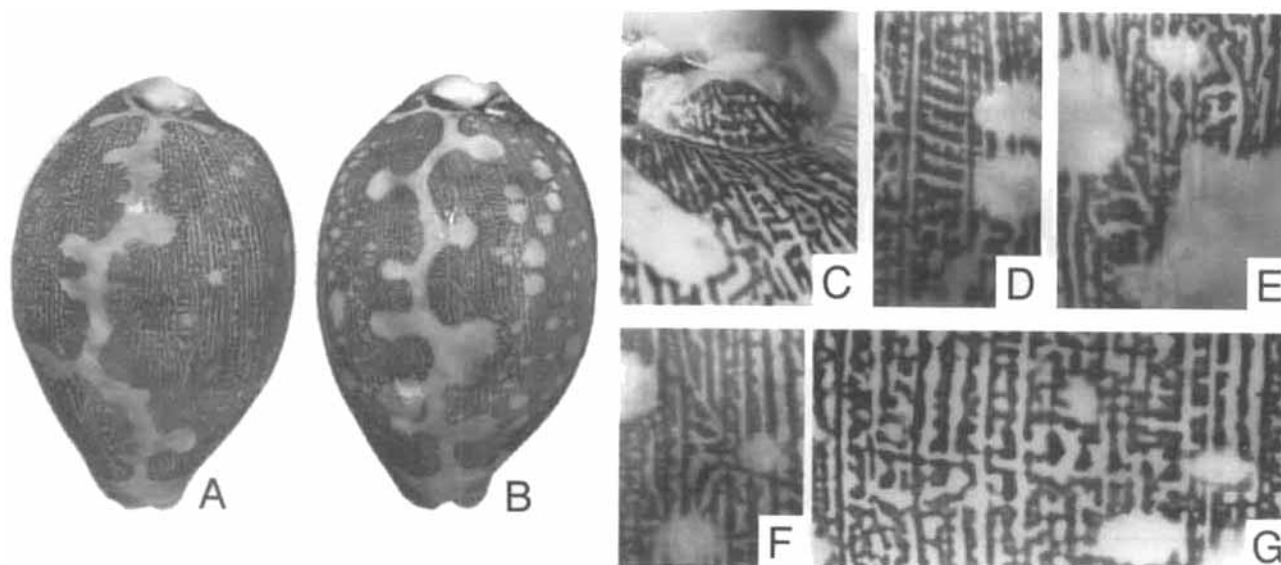


Fig. 3. *Cypraea mappa* Linnaeus, Recent, Cebu Island, Philippines. □A–B. Variability in aspect of the apposition line, $\times 0.75$. □C–G. Anomalies in the orientation of collabral pigment stripes, $\times 3$. See the text for details.

The apposition line can be straight (Figs. 1H–I, 4I–J), undulating or, less frequently, meandering and/or branched. In this last case, considerable individual variation can occur (Fig. 3A–B). Representatives of this type of apposition line were not available alive, but it is reasonable to suppose that the edges of their mantle lobes are incised, furrowed and/or folded, thus yielding the observed line morphology.

Secondary shell thickening in the dorsal region takes place mostly on the inner shell surfaces, and mostly on the outer surfaces in the ventral region (Fig. 5B).

Mantle morphology. – The outer surface of the mantle lobes is either smooth or, more often, covered with large papillae. A broad range of morphologies can be observed in these structures. Dendritic papillae are especially common, but knob-shaped and tentacle-like papillae are also frequent. The papillae are often of a different colour from the surrounding tissues. In a few species, the outer surface of the mantle lobes bears a uniform colour similar to that of the dorsal shell surfaces. In many other species, however, the colours are strikingly different. In several species, the outer mantle surface bears a complex colour pattern (without visible correspondence to the shell's pattern) consisting of patches or stripes. This is true of other cypraeaceans as well. *Volva* and *Cyphoma*, in particular, possess very bright colour patterns on their outer mantle surfaces (unpublished observations). These genera are also remarkable for the absence of colour patterns on their shells.

The surface of the mantle lobes facing the shell can only be observed in anaesthetized or preserved specimens. Studied species with uniform or almost uniform dorsal

shell colour (e.g., *C. moneta*) display no visible relief on the inner surface of the mantle lobes. In several species with an uneven pigmentation of the dorsal shell regions (*C. tigris*, *C. miliaris*, *C. vitellus*, *C. mauritiana* and *C. lynx*), there is a correspondence between shell colour pattern and colour of the facing mantle surface. In *C. mauritiana*, slightly depressed round patches on the dorsal shell surface (see below) correspond to matching relief patches on the mantle.

There is no visible correspondence between the distribution of papillae on the outer mantle surface and that of inner-surface relief, nor between papillae and shell-colour patterns.

Morphology and morphogenesis of the colour pattern

In several species, secondary shell layers deposited on the dorsal surfaces are thin and translucent. This allows the original shell colour to be visible also in adult specimens and is easily recognized in species that bear a spiral (Fig. 1C–D) or divaricate (Fig. 1E–G) colour pattern on the primary shell surface. These colour patterns are uni-dimensional in origin (see also above) and easily distinguishable from those generated by two-dimensional programmes.

As mentioned above, in adult cypraeids the mantle surface is stationary with respect to the shell. Therefore, secondary shell layers are built during an extended period of time, and in some cases their construction consists of two or more phases, which are recorded as successive layers.

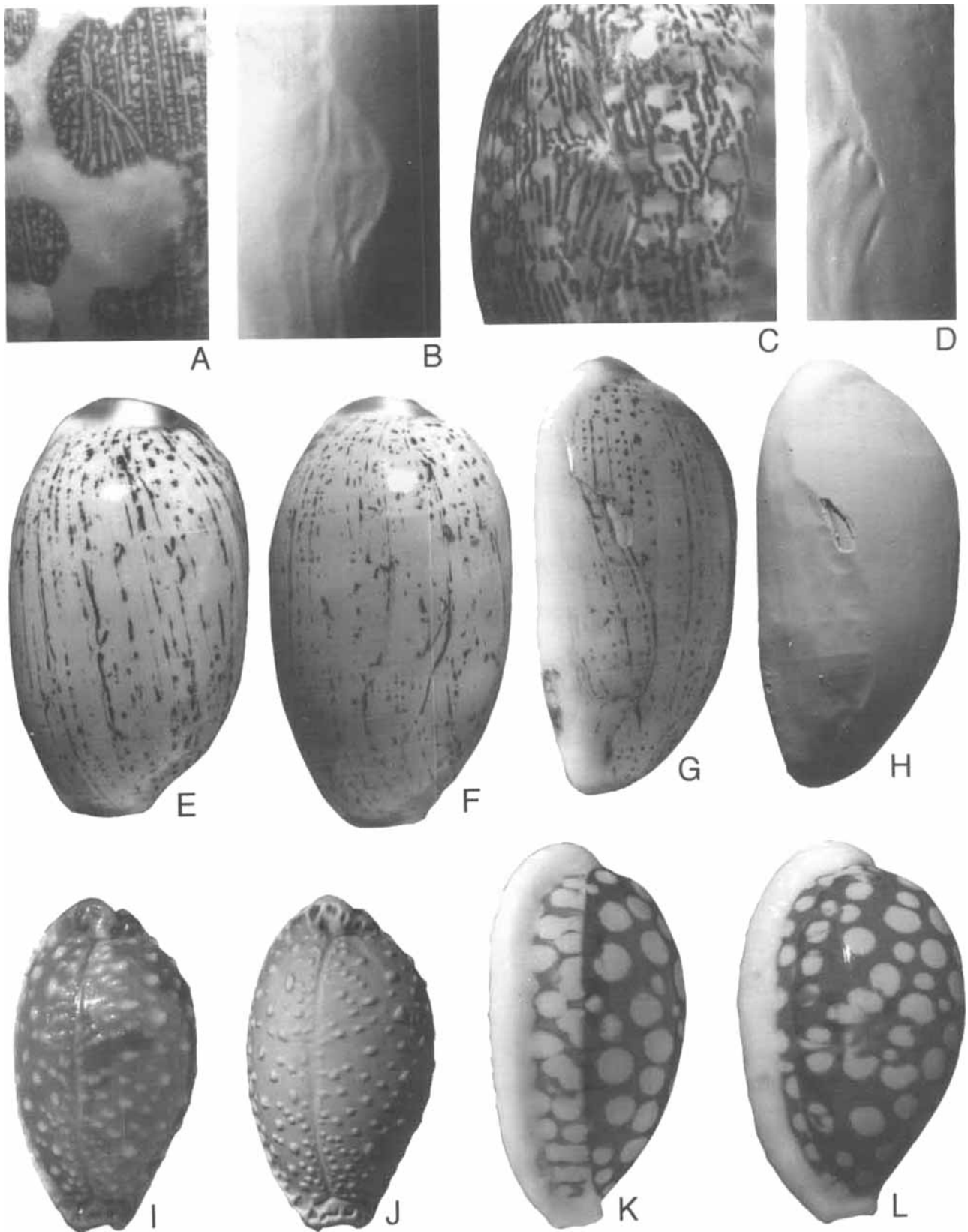


Fig. 4. Recent cypraeids from Cebu Island, Philippines. □A–B. Irregularity in colour pattern of *C. mappa* Linnaeus (A) and associated relief (B, whitened), $\times 2$. □C–D. Irregularity in colour pattern of *C. arabica* Linnaeus (C) and associated relief (D, whitened), $\times 3$. □E–H. *C. isabella* Linnaeus, $\times 3$. Typical specimen (E), specimen with irregular pigment lines (F–G) and associated relief (H, whitened). □I–J. *C. staphylaea* Linnaeus, $\times 3$. Normal pigment pattern (I) and associated relief (J, whitened). □K–L. *C. cribraria* Linnaeus, $\times 2.5$. See the text for details.

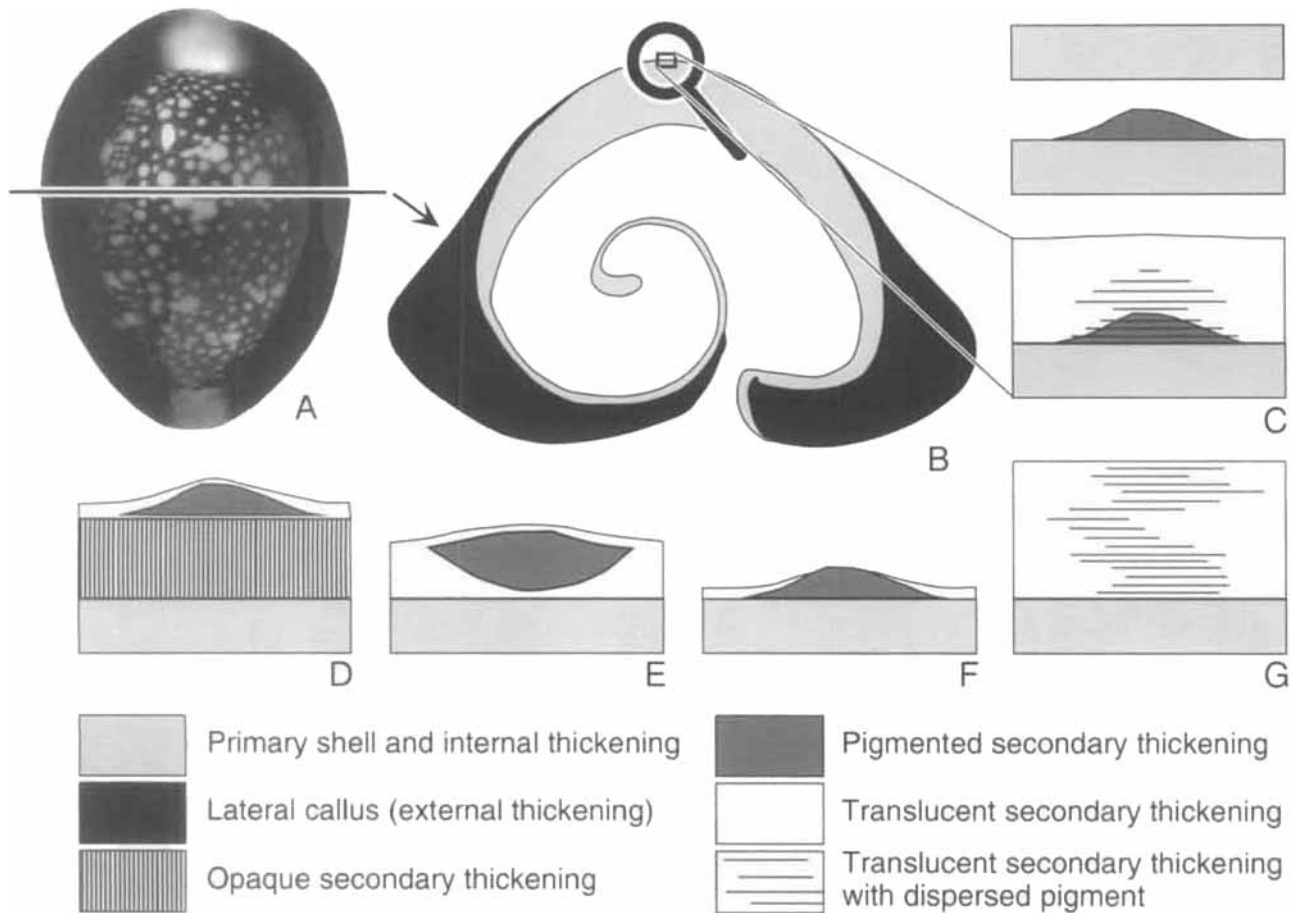


Fig. 5. Recent cypraeids from Cebu Island, Philippines. □A–C. *Cypraea caputserpentis* Linnaeus. A cross-section (B) executed along the shell centre (A) shows the extent of internal versus external secondary thickening. A detail of the dorsal region (C) shows that the dorsal colour pattern is the result of a process consisting of separate stages (C, top to bottom), and that pigmented shell material forms a three-dimensional pattern. □D–F. Cross-sections of dorsal colour patterns in different species (D, *C. vitellus* Linnaeus; E, *C. miliaris* Gmelin; F, *C. histrio* Gmelin) show that there is considerable variation in three-dimensional colour patterns and in their construction processes. □G. Pigmented patches on the thick lateral callus of *C. lynx* Linnaeus slightly change in size and shift position during secretion of the callus, yielding patches with ill-defined perimeters. In C–F, the vertical dimension has been greatly exaggerated for illustration purposes.

In all studied cases, cross-sections show that the visible colour pattern does not originate from an uneven concentration of pigment within a uniform secondary layer of shell material, as in primary colour patterns. Instead, secondary patterns result from the selective deposition of areas of highly pigmented material, which thus forms a three-dimensional secondary structure. In most species, the distinctive dorsal colour pattern is secreted at an early stage and is subsequently 'glazed-over' with a very thin translucent layer (Fig. 5C, F). In a few species (Fig. 5D–E), however, secretion of the pattern follows the secretion of translucent or uniformly opaque material.

On the ventral shell region, a thicker callus is subsequently deposited which often bears a pattern of indistinct pigment patches (Fig. 1D). Secretion of the callus takes place during an extended period of time, and pig-

mented patches appear to change shape and position slightly (Fig. 5G), thus yielding the observed 'fuzzy' outline. Even in this case, pigment is not uniformly distributed and seems instead to occur in very thin lenses.

Significance of anomalies in the study of morphogenesis. – Insight into the normal operation of morphogenetic programmes can often be gleaned from the observation of anomalous or pathologic characters. This indirect approach can be applied when it is not possible or practical to interfere with morphogenetic processes in the course of laboratory experiments.

A survey of several thousand cypraeid shells belonging to over one-hundred-and-fifty species revealed a few distinct categories of anomalies; these are discussed below together with non-pathologic but related features.

'Double-exposure' anomalies. – These features derive their name from their similarity to photographic double-exposures. A double-exposure can be performed by taking two successive shots of the same scene, without advancing the film, with a hand-held camera. The camera will point in a slightly different direction at each shot, the resulting picture consisting of two 'ghost' images marginally shifted in relation one to the other.

A closely similar phenomenon takes place in cypraeids when the position of the mantle relative to the shell shifts slightly during secretion of the colour pattern (Fig. 2B). In the illustrated specimen, pattern secretion had just begun when the disturbance occurred, so one of the two ghost images is weaker than the other. In this species, the apposition line is located near the right edge of the ventral surface. Therefore, a single mantle lobe is responsible for secretion of the whole dorsal pattern. Fig. 1A shows the normal colour pattern of this species.

Disturbances of the mantle that cause this type of anomaly (e.g., contractions or expansions of the mantle tissues) can be localized or affect the entire shell. In extreme cases, displacement of the mantle is so extensive that it is difficult to detect a correspondence between the two sets of pattern elements.

Superposed patterns. – This phenomenon takes place when one of the mantle lobes initially secretes a colour pattern. The other lobe subsequently covers the same shell region and superposes its own, distinct, pattern (Fig. 4K–L). In this case there are no double 'ghost images', but rather two independent and overlapped patterns.

It is possible that this anomaly originates from the two mantle lobes partly overlapping each other along the apposition line. In this situation, a disturbance may reverse their overlapping order, bringing the originally outermost lobe into contact with the shell. It is unlikely that this phenomenon results from a lateral shift in position of the mantle lobes, since that would result in an evident double-exposure anomaly in the surrounding shell areas. This anomaly is especially common in *C. cribraria*.

Growth-line effect. – This is a normal feature of many cypraeid patterns, rather than an anomaly. However, the morphogenetic origin of this phenomenon becomes evident in the presence of shell anomalies. Thin stripes with a prevalently collabral (roughly axial) orientation are a common feature of cypraeid patterns. In *C. mappa*, the overall orientation of these stripes is largely unaffected by proximity with non-pigmented patches and with the apposition line (Fig. 3A–B).

The orientation of axial stripes is sometimes disrupted in a way curiously reminiscent of the growth lines that accompany repair to a dented or chipped shell margin (Figs. 3E–G, 4A–H). In fact, these regions of disrupted colour pattern possess a slight relief, inherited from the underlying surface of the juvenile shell.

The original relief of growth lines is almost completely obliterated by secondary shell layers. However, even minimal changes in relief can be detected by observing the reflections of a point-sized source of light (or of a grid of point-sources) on the shell while slowly rotating it. Unfortunately, this technique is not suitable for photography, and the alternative used in this paper consists of whitening the shells with magnesium oxide and illuminating them with grazing light. Examination with the above methods shows that these disturbances of the colour pattern do indeed follow the relief of underlying shell repair (Fig. 4A–D, G–H). This repair occurred during the juvenile growth phase, while the shell was growing by marginal accretion.

If anomalous growth lines have this effect on the secondary colour pattern, it is reasonable to assume that normal growth lines have a similar effect. This is also confirmed by observations. Thus, the axial orientation of 'normal' colour stripes reflects the orientation of the underlying growth lines. In fact, the colour pattern correctly changes orientation to follow growth lines across the suture between successive whorls (Fig. 3C).

Pigment stripes sometimes follow growth vectors and replicate a corresponding relief of the underlying shell (Fig. 3G). This relief results from point-sized injury to the mantle tissues recorded as a spirally oriented streak or furrow by marginal shell growth.

The above observations indicate that the morphogenesis of secondary colour pattern in *C. mappa* and similar species is controlled by earlier shell relief. However, this is not a complete explanation in *C. mappa*, because its collabral stripes show a stochastically constant reciprocal spacing. Growth lines, instead, become more closely spaced toward either the apical or adapical extremities, since the radius of curvature of the shell (and consequently its linear growth rate) decreases toward these regions. Observation shows that adjacent stripes are periodically suppressed or merged in these regions to maintain a constant reciprocal spacing.

Thus, the relief of growth lines not only controls this colour pattern, it may also act as an initial 'seed' for the morphogenetic programme of the colour pattern. While the programme unfolds, the initial orientation of seed features is largely inherited by the developing pattern, but the reciprocal spacing of pigment lines changes according to the self-organizing rules of the programme (see below).

In *C. isabella* (Fig. 4E–G) the juvenile colour pattern is still largely visible in the adult. However, the adult is characterized by the presence of a few irregular, narrow black stripes. These features follow depressed growth lines (including irregular ones; Fig. 4F–H). Therefore, this pattern is comparable in origin to the one described in *C. mappa*, but it differs in the fact that the stripes are distant from each other and irregularly spaced. So the placement

and reciprocal spacing of these lines is controlled to a greater extent by the underlying relief.

Pigment in *C. isabella* also tends to coalesce into drop-like spots (Fig. 4E–G). This is apparently due to the fact that pigment secretion is initiated by the presence of depressions in the underlying shell, but continues after the depressions are secondarily filled and the relief becomes inverted, causing the pigment to ‘overflow’ into adjacent areas.

False and true meshworks. – The secondary colour patterns of *C. mappa* and *C. arabica* are essentially similar (including the growth-line effect). Non-pigmented patches, however, are more numerous and proportionately larger in *C. arabica*. In this species, collabral stripes are sometimes darker near the non-pigmented patches. This produces the superficial impression of a meshwork of stripes parallel to the edges of the patches. However, the individual stripes composing the pattern follow the collabral orientation of growth lines.

In the superficially similar *C. depressa*, on the other hand, the pattern is a true meshwork, and there are no collabral lines. *C. grayana* is morphologically intermediate between these two species, since its pattern contains both types of elements.

Meshworks differ also in the proportion of pigmented versus non-pigmented surface. In *C. histrio*, the pigmented lines form a very thin mesh surrounding large patches. In species like *C. mauritiana* (see also below), non-pigmented patches are irregularly distributed onto a predominantly pigmented background.

‘Thick-paint’ effect. – In several cases, a small amount of relief (detectable with the methods discussed above) accompanies the colour patterns of adult cypraeids. For instance, the pattern in *C. mauritiana* (Fig. 2C) consists of non-pigmented oval ‘windows’ (through which the juvenile colour pattern is visible) on a heavily pigmented ‘background’. When relief is observed, the pigmented background actually turns out to be in relief, like a layer of thick paint, with the windows sunken in it (Fig. 2D).

The illustrated specimen also shows an instance of ‘double exposure’, visible along the edges of the windows (Fig. 2C–D). The lesser-pigmented regions bordering part of the window periphery correspond to a lower thickness of the pigmented layer. Thus, this type of pigmentation is in effect three-dimensional, since its appearance depends on the variable thickness of a uniformly pigmented layer (as observable in cross-sections), rather than on a spatially non-uniform concentration of pigment in the shell material. Combined with a partial translucency of the pigmented layer and a different colour of the original shell surface, this results in the observed pattern.

In *C. mauritiana*, the mantle tissues facing the dorsal regions of the shell bear a relief inverse to that of the shell. Other species bearing similar colour patterns were not

available alive, but it is reasonable to suppose that they possess a comparable mantle relief. The ‘thick-paint’ effect with non-pigmented windows sunk into a pigmented background is also observed, to varying degrees, in *C. cribraria*, *C. cribellum*, *C. gaskoini*, *C. catholicorum*, *C. leucodon*, *C. esontropia*, *C. maculifera*, *C. depressa*, *C. cervinetta*, and *C. cumingii*.

In a few of the above species the background surrounding the periphery of the windows is thicker and more heavily pigmented than further away from the window. This suggests a mechanical interpretation: when the mantle is pressed against the shell surface, the edges of the relief patches on the mantle cause a ring-shaped cavity to form around the perimeter of each patch. Fluid secreted from the mantle epithelium tends to flow from surrounding regions and to collect into this cavity, where it deposits a larger amount of pigmented material than in surrounding areas.

In *C. camaleopardalis* the opposite colour pattern is observed: pigmented patches stand out in relief above a non-pigmented background through which the original shell colour shows. The same is true of the rings in *C. argus* and of the meshwork in *C. mappa* and *C. histrio*. In *C. cicercula*, *C. staphylaea* (Fig. 4I–J) and *C. limacina*, patches are thick enough to be regarded as nodules or tubercles. Although these patterns are the opposite, in relief, of the windows discussed above, they may well have the same morphogenetic origin. In fact, a morphogen may trigger pigment or shell-material secretion by either its presence or absence.

In several of the above species, short transversal ridges are present, especially along the border with the ventral callus on the right side of the shell. Occasionally, nodules on the dorsal surfaces are locally elongated into short stripes (Fig. 4I–J).

In *C. nucleus* (Fig. 1H) and *C. granulata*, nodules are interspersed with ridges that originate as extensions of the apertural teeth and reach up to the apposition line. Sometimes nodules appear to function as ‘attractors’ to ridges, which preferentially run from nodule to nodule. In *C. capensis* and *C. childreni* (Fig. 1I–J), and in the superficially convergent Triviidae, only ridges are present. As discussed below, simple changes can make the same morphogenetic programme generate either stripes or spots (or intermediate patterns). At least in some species, like *C. nucleus*, nodules appear to be secreted first, followed by ridges. This process would involve two simple morphogenetic programmes acting in sequence, rather than a single complex programme co-ordinating two types of elements.

While the occurrence of sculpture in some Cypraeidae is a well-known fact, no attention has apparently been paid in the literature to the relationships between sculptures and colour patterns. It is reasonable to regard dorsal cypraeid sculptures as a specialized case of the three-

dimensional colour patterns discussed above. This provides a simple evolutionary explanation to the otherwise baffling presence of a few instances of well-organized sculptures (including the unique spines of *Gisortia*; see above) in a family of otherwise smooth forms.

Computer modelling of cypraeid stripe patterns

Algorithm. – The choice of an algorithm for modelling two-dimensional colour patterns may rest on several considerations. As pointed out by H. Meinhardt (personal communication, 1995), a few of the available algorithms (including the one chosen for the present paper) introduce artificial-looking parameters and conditions in order to generate self-organizing patterns. Other algorithms, on the other hand, are more likely to reflect the biochemical dynamics of morphogenetic processes. The latter category of algorithms is obviously preferable when the objective is to model a process at the molecular level. However, these algorithms are usually mathematically complex and computation-intensive. Since the goal of the present paper is a visual comparison of the results of computer simulations with actual patterns, I chose to use a simpler algorithm that has already been used in the literature for a similar purpose (albeit in a different taxonomic group; see below).

The program used for this paper is similar to the one written by Kondo & Asai (1995). The mantle surface is represented by a two-dimensional array of square cells. The colour of each cell is controlled by the local concentration of an activator substance (A). The concentration of the activator, in turn, depends on its diffusion and decay constants (DA and gA , respectively), and on its synthesis rate. In order for the system to generate a self-organizing pattern, the presence of an inhibitor (I) with its own set of constants (DI and gI , respectively), is necessary. The concentrations of the activator and inhibitor are given by

$$\frac{dA}{dt} = c_1A + c_2I + c_3 - DA \frac{d^2A}{dx^2} - g_A A$$

$$\frac{dI}{dt} = c_4A + c_5 - DI \frac{d^2I}{dx^2} - g_I I$$

where $c_1..c_5$ are constants.

The following constraints force the synthesis rates of activator and inhibitor to remain within realistic ranges:

$$0 < c_1A + c_2I + c_3 < S_{A_{max}}$$

$$0 < c_4A + c_5 < S_{I_{max}}$$

where $S_{A_{max}}$ and $S_{I_{max}}$ are maximum allowed values.

As pointed out by Kondo & Asai (1995), other types of reaction–diffusion kinetics do not require external constraints. However, the kinetics shown above (originally formulated by Turing 1952) are simpler and faster to implement in a computer program.

In software, differential equations are approximated to finite difference equations, and the procedure consists of a number of cycles, each consisting of a diffusion and a reaction stage. For a cell of co-ordinates (i, j) , one cycle can be expressed as:

diffusion:

$$A'_{i,j} = (1 - 5D_A)A_{i,j} + D_A(A_{i-1,j} + A_{i,j-1} + A_{i+1,j} + A_{i,j+1} + (A_{i-1,j-1} + A_{i-1,j+1} + A_{i+1,j-1} + A_{i+1,j+1})/4)$$

$$I'_{i,j} = (1 - 5D_I)I_{i,j} + D_I(I_{i-1,j} + I_{i,j-1} + I_{i+1,j} + I_{i,j+1} + (I_{i-1,j-1} + I_{i-1,j+1} + I_{i+1,j-1} + I_{i+1,j+1})/4)$$

reaction:

$$S_{A_{i,j}} = c_1A'_{i,j} + c_2I'_{i,j} + c_3$$

$$S_{I_{i,j}} = c_4I'_{i,j} + c_5$$

$$\text{constrain}(S_{A_{i,j}}, S_{I_{i,j}})$$

$$A''_{i,j} = (1 - g_A)A'_{i,j} + S_{A_{i,j}}$$

$$I''_{i,j} = (1 - g_I)I'_{i,j} + S_{I_{i,j}}$$

where A' and I' are the concentrations after diffusion, S_A and S_I the synthesis rates, $\text{constrain}()$ the constraint function discussed above, and A'' and I'' the new values. The program is run until the pattern becomes visibly stable (in the simulations shown in Fig. 6, usually 1,000–2,000 cycles).

As discussed by Meinhardt (1989), a threshold exists in the effects of the synthesis rate of activator. Above this threshold, the pattern consists of patches (or of a meshwork with holes, if the activator is considered to promote colour-secretion by its absence). Below the threshold, the pattern consists of alternating light and dark stripes of equal thickness (see also Fig. 6B–D, and below).

Unless otherwise indicated in the text, the values used for the models discussed below are:

$$DA = 0.007 \quad c_1 = 0.08 \quad S_{A_{max}} = 0.18$$

$$DI = 0.1 \quad c_2 = -0.08 \quad S_{I_{max}} = 0.5$$

$$c_3 = 0.05$$

$$g_A = 0.03 \quad c_4 = 0.1$$

$$g_I = 0.06 \quad c_5 = -0.15$$

Pattern characteristics. – Self-organizing patterns arise from the above kinetic system in the presence of disuniformities in the initial state of the cell population. Disuniformities can be created by ‘seeding’ the population with an initial pattern (see below), or by adding a small amount of random noise in the initial concentrations of activator and inhibitor in each cell, as done in Fig. 6A. The

program automatically adjusts the contrast of the display to the minimum and maximum concentrations of morphogen throughout the cell population. (Fig. 6 shows the activator concentration.) Without this adjustment, Fig. 6A would be almost uniformly white, because the absolute value of noise is quite low.

In the lack of disuniformities, the cell population continues to oscillate synchronously between dark and light states or, depending on the values of the constants, settles into either state. In the presence of disuniformities, synchronous oscillations occur in the initial stages, but settle shortly thereafter.

When only initial noise is present, details of the pattern are unique and depend on the local noise values. The general aspect of the pattern, however, is controlled solely by the morphogenetic constants of the system. In particular, Fig. 6B–D show the results of altering S_{Amax} (values are 0.18, 0.23 and 0.28, respectively). At increasing values of S_{Amax} , stripes become gradually replaced by spots.

When only an initial pattern (without added noise) exists, it will progressively spread its influence to the whole cell population (Fig. 6E–G). In the simultaneous presence of noise, however, the initial pattern will not spread beyond a certain distance (Fig. 6H). The similarities of the patterns in Fig. 6F–H with those generated by oscillating chemical reactions and by expanding rings on the surface of water is only superficial. In fact, the circular stripes in Fig. 6F–H do not actually move outwards (as in chemical and mechanical waves). In addition, like chemical waves but unlike mechanical waves, two morphogen gradients that move toward each other obliterate each other on contact, instead of crossing and moving further.

Assumptions. – In applying the above kinetics to model the growth-line effect in cypreaids, one must assume that the initial concentrations of activator and/or inhibitor are affected by the presence of minute shell relief. One way this could be mediated is by an uneven distribution of fluid secreted by the mantle in the space between the mantle epithelium and the shell. Such a fluid, even if uniformly secreted by the whole mantle surface, would accumulate in depressions of the shell surface. Another way is by mechanical or chemical feedback caused by local stretching and/or compression of the mantle tissues when these are pressed against an uneven shell surface.

Once the pattern has reached a stable state, it remains stable even if the initial relief-based cue is removed (see also above). This situation does indeed happen once secondary shell secretion covers the original shell surface.

Modelling the growth-line effect. – The cell population can be ‘seeded’ with an arbitrary pattern designed to model the presence of growth lines. In the simplest case, this is done by changing the activator and/or inhibitor concentrations along one or more lines of cells (e.g., Fig. 6I, M,

Q). Comparable results are obtained by using other seeding conditions, some of which (H. Meinhardt, personal communication, 1995) may be more realistic in biological terms. This aspect of the problem may be worth further investigation but would rather be straying from the scope of this paper.

The result of adding growth lines is a pattern of stripes which tend to remain nearly parallel to adjacent stripes as well as to the initial lines (Fig. 6J–L). The final reciprocal spacing of these stripes, however, is not controlled by the initial position and spacing of the seed lines. When these are very close to each other, they merge into a single stripe. When they are distant from each other, new stripes are intercalated. The final pattern is also insensitive to the absolute values of the initial concentrations of activator and inhibitor along the seed lines.

Results become more complex when curved seed lines (meant to model shell repair) are added (Fig. 6I, M, Q), or when seed lines have different orientations (Fig. 6S). In particular, one may notice a frequent alternation of regions of different thickness along a stripe, as well as the appearance of small aligned patches between adjacent lines (Fig. 6N–P, R, T). Interestingly, both features are also common in *C. mappa* (Fig. 3). Another feature predicted by the model and present in *C. mappa* is the roughly equal thickness of pigmented and non-pigmented stripes.

An unexpected result is that, in the presence of seed lines, patterns obtained in a short time (a few hundred to a few thousand cycles) are little affected by the value of S_{Amax} . Fig. 6N and 6O show the results with $S_{Amax}=0.18$ and 0.28, respectively. By comparison, the patterns produced by the same values in the exclusive presence of random noise are very different (Fig. 6B, D, respectively; see also above). At high values of S_{Amax} , however, by allowing the process to continue for a longer time (tens or hundreds of thousand cycles) one can observe stripes that very slowly break down into spots. This process begins in areas where stripes bifurcate or sharply bend. The addition of random noise to the seed lines (Fig. 6P versus 6N) has very little effect (except in regions that are sufficiently far from the seed lines to be controlled only by noise).

In the models, as well as in *C. mappa*, a variety of geometric figures is present in the narrowest portion of the stacked-V structures triggered by convex growth lines (Figs. 6L, N–P, R, 3E–F). The presence of small areas with stripes oriented perpendicularly to the prevalent direction is also correctly modelled (Figs. 6T, 3D). These regions likely originate from one or more spiral furrows, and/or from the local absence of growth lines.

The situation is different in *C. teres* (Fig. 4E–G), in which stripes are almost exclusively found in correspondence of depressed growth lines and are much narrower

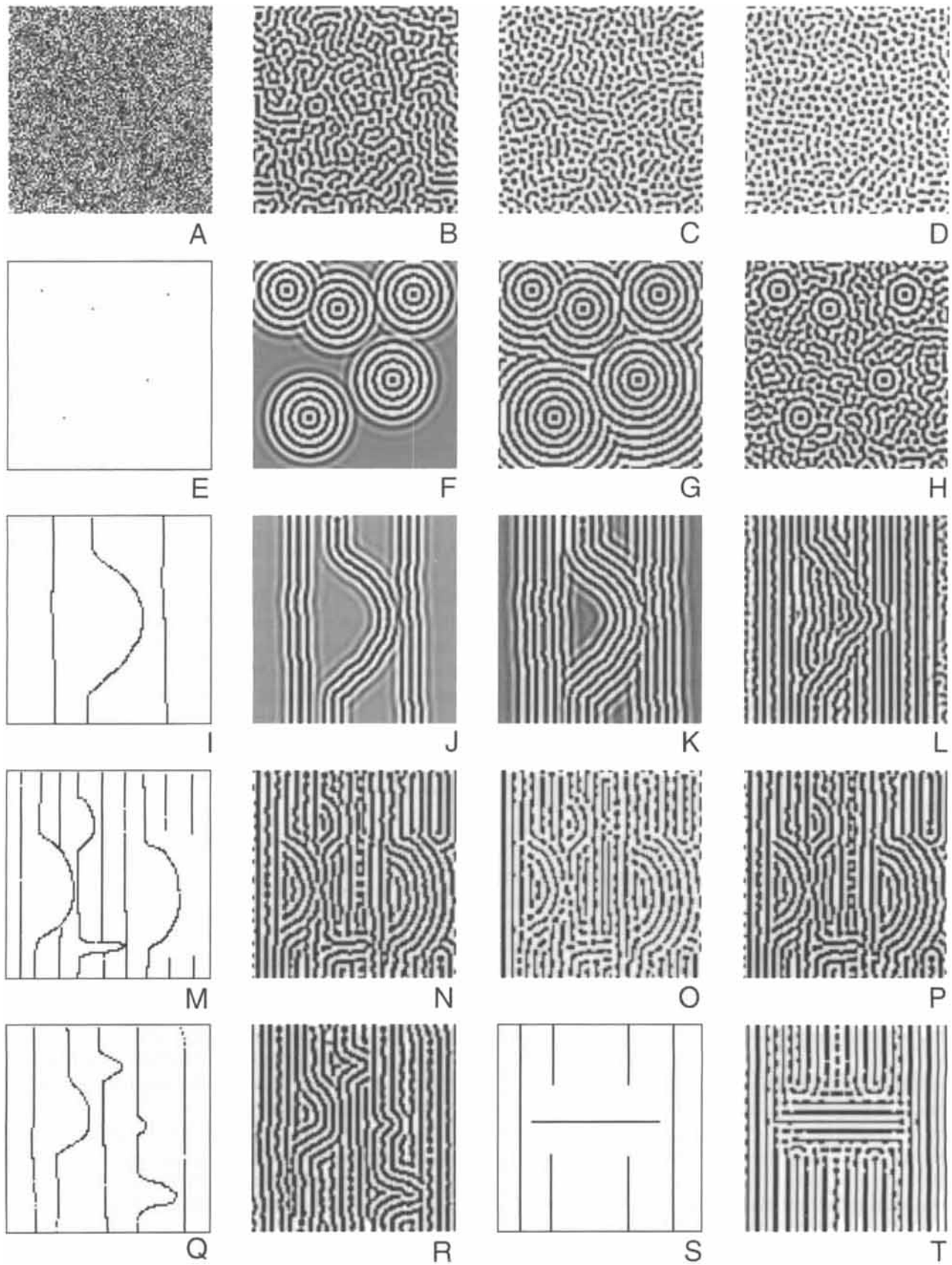


Fig. 6. Computer models of two-dimensional pigment patterns. See the text for details.

than the adjacent non-pigmented areas. In addition, pigmented stripes are usually not continuous, but rather break down into aligned patches. This points to a different morphogenetic programme, in which the pattern is not self-organizing (at least on a large scale) and does not propagate outside its source region.

Considerations on morphogenesis

Origin of meshworks. – True meshworks cannot be modelled by the above dynamic system and require a more complex model. However, cypraeids with meshwork patterns display a rare anomaly in which a small pigmented spot is present roughly at the centre of each non-pigmented patch (Fig. 2E). The partial similarity of this anomaly with Fig. 6H does suggest that the morphogenetic programme of non-pigmented spots is partly similar to the one discussed above.

It may be further noticed that the central spot in these anomalous patches is weaker and thinner than the surrounding collabral stripes. This, in turn, suggests that non-pigmented patches originate from a programme very similar to, or identical with, the one generating collabral stripes. After an initial phase, however, a second programme takes over in correspondence of the non-pigmented patches. A delay in the onset of this second programme would cause the observed anomaly.

A mechanical, rather than biochemical process could explain some of the meshworks or hole patterns (especially those associated with a thick-paint effect). As shown in Fig. 7, the presence of papillae on the mantle surface facing toward the shell may result in the formation of a ring-shaped cavity, in which fluid secreted by the mantle may collect and subsequently deposit pigmented shell material. Such a process need not to be an alternative to morphogenetic programmes, since both mechanisms may be at work simultaneously (besides, the distribution of papillae is likely under morphogenetic control, which may thus be the ultimate cause of the pattern, mediated by mechanical fluid containment).

Origin of ridge sculptures. – It is interesting to note that ridge sculptures (e.g., Fig. 11–J) appear to use the teeth located on the inner and outer shell lips as a morphogenetic cue. In fact, ridges almost invariably develop as an extension of these teeth. When the reciprocal spacing of the ridges exceeds a threshold value, new and thinner ridges are intercalated (Fig. 11–J). This situation is very similar to growth of the colour pattern described by Kondo & Asai (1995) in the fish *Pomacanthus semicirculatus*. Although adult cypraeids, unlike fish, do not grow, the ridges diverge slightly when they extend from the apertural teeth toward the dorsal shell region, and their reciprocal spacing does therefore increase.

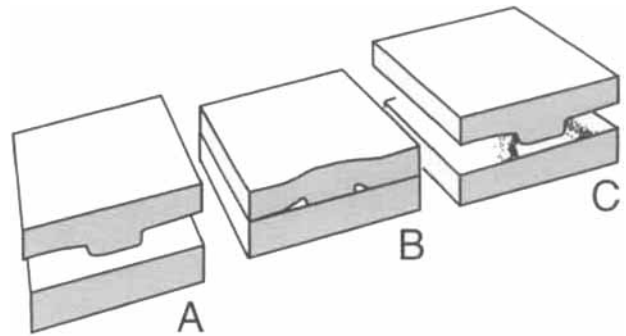


Fig. 7. As an alternative to morphogenetic programming, some of the ring-shaped patterns may result from a mechanical cause. A papilla on the mantle surface (A, uppermost) facing the shell produces a ring-shaped cavity when the mantle touches the shell (B). Pigment-containing fluid secreted by the papilla collects in this cavity and deposits to form a ring-shaped, pigmented relief (C).

Possible functions of colour patterns

Little is known of the adaptive significance of colour patterns in gastropods, and no paper known to me deals with the function of cypraeid colour patterns. Savazzi (1994) showed a clear correlation between sediment colour and shell colour in populations of a few species of *Oliva*. Shell colour may have a camouflaging function in other gastropods as well. In cypraeids, the colour of the shell is generally quite unlike that of the sediment. The mantle of some epifaunal cypraeids may have a camouflage function (e.g., Taylor 1979). In most cases, however, shell colour is far from cryptic.

Acid secretions produced by the papillae located on the outer surfaces of the mantle lobes are likely to have a repellent function (Taylor 1979). Therefore, shell and/or mantle colour may serve to 'advertise' these organisms and make them easily recognizable by predators, which would thus learn to avoid them. At least in some cases, it is possible that bright mantle and/or shell colour patterns of cypraeaceans cause predators to confuse them with nudibranchs (which often carry nematocysts, are brightly coloured, and possess appendages superficially similar to the mantle papillae of cypraeids) or other organisms (e.g., coelenterates) that live in the same environments (unpublished observations).

Complex colour patterns may also disrupt the perception of the shape of the mollusc, thus making it difficult for predators to detect. As an alternative hypothesis, in cypraeids with different mantle and shell colours (which is the rule), the sudden withdrawal of the mantle, following attack by a predator, exposes a shell of completely different appearance. This could well confuse a visually hunting predator, and induce it to believe that the organism it was attacking managed to escape. Finally, the possi-

bility that shell colour might have a function in the recognition of conspecific individuals could be worth testing.

It must be stressed that none of the above explanations has been experimentally verified. It may be noted, however, that the computer model discussed above indirectly suggests that cypraeid patterns do have an adaptive value. In fact, only a small proportion of the combinations of realistic values for the constants yield a pattern. Most of the combinations yield either a uniformly non-pigmented or a uniformly pigment-saturated surface. Therefore, if the values of the constants were allowed to evolve at random (as is reasonable if considered to be neutral characters), we would expect most cypraeids to bear a uniform colour. This, however, is far from reality: a quick review of the literature shows that, among the roughly 200 Recent cypraeid species, at least 190 possess very visible colour patterns (either primary or secondary). The remaining species (with the exception of rare albino populations of normally pigmented species) possess no proper pattern but do display colour spots or coloured areas in specific regions (especially 'eye' spots on the anterior and posterior canals).

Conclusions

The colour patterns of adult cypraeids are generated by two-dimensional morphogenetic programmes and consist of three-dimensional structures. Disturbances of the construction process result in characteristic anomalies, totally different from those observed in one-dimensional programmes. The two-dimensional programmes of cypraeids are often controlled by three-dimensional relief of the underlying shell. In several species, the presence of growth lines on the surface of the juvenile shell is a prerequisite for the formation of the adult colour patterns characteristic of the species. It is also likely that relief of the mantle tissues facing the shell has an effect in controlling the colour pattern.

Cypraeid colour patterns are three-dimensional, rather than two-dimensional. Their appearance often depends on the uneven thickness of an evenly pigmented shell layer, rather than on, or in addition to, a spatially uneven concentration of pigment material. These three-dimensional colour patterns are a straightforward stepping-stone to the evolution of true sculptures (knob and/or ridge patterns in several cypraeids; isolated spines in *Gisortia*). This provides a simple evolutionary explanation

to the presence of a few highly-sculptured representatives in a family of generally smooth forms.

Computer modelling of stripe patterns as the result of a reaction-diffusion system involving an activator and an inhibitor is successful in reproducing several characteristics observed in actual cypraeid shells. Computer models also show that most of the realistic combinations of morphogenetic factors do not produce a pattern. Therefore, the almost ubiquitous occurrence of colour patterns in the Cypraeidae can be expected to have a yet unclear adaptive value.

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