COLOUR PATTERNS IN THE GENUS *OLIVA*. AN ATTEMPT TO SIMPLE ANALYSIS AND INTERPRET ATION.

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ABSTRACT.

An elementary model, based upon a "cellular game", can simulate the formation of most of the isolated elements found in *Oliva* shell patterns. These are shown to be chevrons or simple chevron derivatives. It predicts the interaction between chevrons and thus allow the description of local patterns in simple quantitative terms. Taxonomic applications are considered.

INTRODUCTION

The colours and the colour patterns of mollusc shells have always fascinated humans by their sheer beauty. In addition to inspiring artists, colours and patterns have also been of great importance for taxonomists and still constitute a large part of contemporary descriptions and diagnoses of molluscs. These characters deserve special consideration because they have been the source of many taxonomic errors. There are two main problems with colour characters: variability and complexity.

Variability

One of the main biological causes of the old "*Oliva* problem" is certainly the well-known striking *variability* of the colours and colour patterns of many species. We will restrict our examples to the genus *Oliva,* with which the authors are more familiar, but a similar situation can be found in many species of other groups of molluscs (such as *Conus, Voluta, Neritina, Tapes, Polymita* to cite a few).

Differences in the colour pattern of *Oliva* shells can result from:

* interspecific variation (between specimens of different species)
* intraspecific variation (between specimens of a same species), with several components:
  (i) interpopulation variation (between populations of a same species)
  (ii) intrapopulation variation (between specimens of a same populations)
  (iii) ontogenetic and accidental variations (during the lifetime of an individual).

This is true for the variability of any feature and should not be forgotten when analysing the especially complex colours and patterns in the genus *Oliva.* Quite different patterns can indeed be found in specimens of a same species. In many species, specimens can also, in addition to their "normal patterns", masquerade in all white, all yellow or all black colour forms. So, colours and colour patterns are optional characters, leading to polythetic classifications. The taxonomic interpretation of such optional features requires special caution (see Tursch 1998). Nevertheless, the taxonomist should not disregard the study of colours and colour patterns. In a group of shells of quite homogeneous shape, colours and colour patterns are what people really see. These features afford the first clues for quick species recognition, often effective because even the most variable *Oliva* species have a large but finite "repertoire".

Complexity: what do we see?

The nature of what we see is complex: it is the additive effect of different patterns occurring in different crystal layers of the shell. The final aspect depends on the col-

our and concentration of the pigments, the thickness and the transparency of the layers. So the colour of the pigments in the shell is not necessarily identical to the coloured impression perceived by the observer looking at the shell.

When covered by thick overlaying enamel, a pigment will appear more bluish or greyish and the pattern will appears more diffuse and blurred. An *Oliva* pattern that appears sharply delineated to the naked eye has quite blurred edges when observed under even moderate magnification. The thickening of layers during growth can sometimes completely hide a pattern, as shown in Fig.1.

The depth at which pigments occur is also probably responsible for the separation of blue and orange patterns (OBS: Orange-Blue Separation) commonly observed in (and often a characteristic of) several Indo-Pacific *Oliva* species (see Greifeneder, 1981; Tursch, Greifeneder & Duchamps 1999).

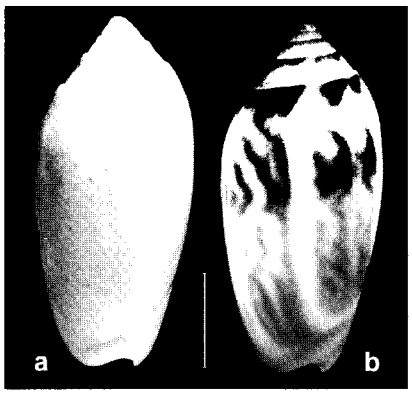

Figure 1. Colour patterns can be hidden. *Oliva spicata* (Röding, 1798), Baja California, W. Mexico. Scale bar: 10 mm. The same specimen is seen. a: in usual conditions, reflected light. b: in transparency, illuminated from the back.

In any case, colours and patterns are two different things. Both are variable but they do not necessarily vary in the same way. So far, it is not clear that there is any relation between a given pattern and its colour.

Problems with colours

First there is a problem with colour description. Colours could be accurately reported, for instance by using conventional colour charts. But so many colour nuances can be found on one single *Oliva* shell that only a few could be described in practice. Colours are also perceived and described differently by different people. The comparison of descriptions with well-preserved type material shows that some famous authors were colour blind, a sex-related inherited disorder.

The large variety of colours displayed by *Oliva* species seems to derive from only a few constituents. Sections in *Oliva* shells show only pigments in the yellow-orange-brown-black series. Blue and green pigments are rare (if present at all). Chemists have intensively studied the coloured secretions of some molluscs, such as the dyestuffs of the indigo family (the famous antique purple) found in some Mediterranean Muricids. Much less is known about shell colours: the chemical structure of none of the *Oliva* shell pigments has yet been reported. Simple tests (for instance treating the shells with hydrochloric acid) show that the molecules probably belong to very different categories.

Petuch & Sargent (1986: 4) state that "... shell color is often affected by animal habitat or diet". One often reads that that shell colour is usually produced by porphyrin compounds which derive from waste products in the animal diet. Consequently, populations of the same species dining on radically different food could be differently coloured (Petuch & Sargent, 1986: 8). In experiments on *Oliva* kept in aquaria we could so far not detect any effect of diet on colour. This could be expected because *Oliva* are non-specialised feeders, eating about any prey they can lay their propodium on.

In contrast, there is much evidence on the effect of environment. In many cases, colour variations are related to habitat (Van Osselaer *et al.*, 1993; Tursch, 1998) and colour changes can be experimentally induced (just by putting specimens in another substrate, see Tursch, Ouin & Bouillon, 1995).

For taxonomists, this raises a serious problem of interpretation. *Oliva* colours are related not only to a given gene pool; they can also depend on ecology and ethology. They are even related to the accidents in the life history of a given specimen. In consequence, for taxonomic purposes, it appears therefore much safer to use colour arrangement (the colour patterns) rather than the colours themselves.

Problems with patterns

The colour patterns of many *Oliva* Shells are often very intricate. They defy accurate verbal description (and different authors possibly do not use the same words exactly in the same meaning). At first sight, they appear very difficult to quantify or even to code.

There is an additional difficulty with pattern descriptions. All *Oliva* specimens being different, what should be really described is not the pattern of an individual shell but its 'style' (the program that produced the pattern). This is generally done by visual inspection followed by an "aesthetic analysis", often unconscious and without explicit rules. It is the same procedure that leads us to recognise (or rather think we recognise) that a painting is by the hand of Corot. The system might be quite effective for a true expert but is very difficult to explain in words. It is also open to error, as attested by the large number of fake Corots.

Another, far superior way of reporting the 'style' of a shell pattern could be a causal approach: give the program (and the numerical parameters) from which a whole pattern actually results. The mathematics of this approach could of course be quite complex.

Another way yet could be a simpler descriptive quantitative approach: find a simple, heuristic model, with a restricted number of comprehensible parameters, simulating individual pattern elements and their interaction. Very little has yet been done in this perspective.

In any case, pattern analysis can be done at two different levels: global patterns and isolated "pattern events". The latter, being much simpler, offer better prospects to the taxonomist.

How are patterns produced?

We now have a very good hypothesis on this, thanks to the work of Hans Meinhardt. His wonderful book 'The Algorithmic Beauty of Sea Shells' (1995) is a must in every conchologist's library. It presents a convincing mathematical model explaining the origin of colour patterns in shells. The book is splendidly illustrated and the comparison of numerous computer simulations with actual patterns is most impressive.

In the model of Meinhardt (1995), patterns are historical records of what happens at the shell edge and result from a dynamic system. An essential element of dynamic systems is a positive feedback that self-enhances the initial deviation from the mean; sooner or later, self-enhancing processes evoke antagonistic reactions. The observed patterns thus result from a balance between self-reinforcing and antagonistic tendencies.

A decisive parameter in a dynamic system is the spread of its components, hence the idea of using reaction-diffusion mechanisms. A short-range substance, the activator, promotes its own production (autocatalysis) as well as that of its rapidly diffusing antagonist, the inhibitor.

Three factors play a major role in the changes of concentrations:

(**1**) the rate of production
(**2**) the rate of removal (or decay)
(**3**) diffusion (the loss or gain due to an exchange with neighbouring "cells").

Depending on supply, such an activator-inhibitor system can be oscillating. The system can be described by a set of differential equations, with properly selected parameters. The book comes with a CD of programmes, so the reader can make patterns by himself. The Meinhardt model does deal with many complex situations, so we will only underline here its very essential implications.

(**i**) In the simplest case, a "cell" with a high activator concentration "infects" one

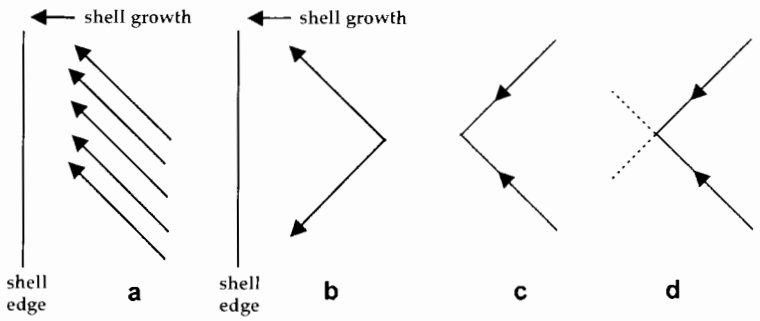

Figure 2. Meinhardt's reaction-diffusion model, outcome of simplest cases. a: parallel pattern obtained by "infection" of one neighbouring "cell". b: diverging pattern obtained by "infection" of two neighbouring "cells". c: when two waves collide, they anihilate each other and do not cross each other as in d.

neighbour cell and the time record of this process can be, for instance, a pattern of parallel pigmentation lines oblique to the growing edge of the shell (see Fig, 2a).

(**ii**) If two neighbours are infected, two waves are initiated, that run in opposite directions, forming a V-like pattern of two diverging lines (see Fig. 2b).

(**iii**) Important observation: when two waves collide, they annihilate each other (see Fig. 2C, d).

Increasing complexity of initial conditions (with one or two modifying patterns) allows simulation of increasingly complex patterns. More complex patterns (such as wavy lines) can be simulated by superposition and synchronisation of stable and oscillating systems, etc. Other patterns require a second, highly diffusible antagonist. Crescents and triangles occur if two inhibitors act in an additive way. Changing wave speeds during collisions yield rounded networks.

The computer simulations of Meinhardt produce very credible imitations of whole (or large portions of) actual patterns. The model is causal, fits well in the present line of thoughts on morphogenetic fields and it probably explains how the formation of patterns actually takes place. So, if the problem is solved, why should we waste time with more considerations about patterns?

The System of Meinhardt explains patterns but (paradoxically) is difficult to apply to pattern analysis. It does not address the pattern details (or isolated pattern events) which happen to be the most relevant for taxonomy. Furthermore, if deriving patterns from parameters is automatically done by a computer program, the opposite problem (deriving parameters from patterns) is not. For intricate patterns, the equations can become quite complex (not necessarily the delight of every taxonomist). Meinhardt himself warned that

Minute differences in the initial conditions can cause a completely different outcome

Sometimes two different models can yield the same pattern with reasonable agree ment.

So the model of Meinhardt can not lead to taxonomic applications (and the author wisely refrained from suggesting any)

SIMULATING ISOLATED PATTERN EVENTS

If we could reduce complex *Oliva* patterns into simple, easily recognised components, these would be far easier to describe Such an approach could possibly afford meristic or measurable taxonomic characters.

It is convenient to consider that any portion of the surface of the shell consists in imaginary "cells". This arbitrary partitioning of space is commonly used in many "cellular automata", such as Conway's famous "game of life". Let us first look at patterns in the central part of the *Oliva* body whorl, where growth lines are parallel. If the shell is assumed to grow at a constant rate (set here at the value 1, for simplification), this central part of the shell can be assumed to

be formed by square imaginary "cells".

What follows is a game that we call the "*Oliva* game". At this stage it is only a game, a way of "painting" selected cells on a grid. It produces credible simulations of the patterns we see on *Oliva* (and many other) shells. The "*Oliva* game" does not require powerful computers grinding complex systems of differential equations. It can even be played with a ruler and compasses, on any piece of cross-ruled paper. Of course, if one uses a computer with a drawing program, things can go much faster. Many of the ideas underlying the "*Oliva* game" originate from the observations of Meinhardt.

Rules of the game

Although the "*Oliva* game" has only four rules, it can simulate patterns of great apparent complexity.

Rules 1 and 2 govern the formation of pattern elements. They concern especially the "micro" level of interpretation.

RULE 1. Starting points can be initiated only in "cells" at the shell edge. Starting points emit an activation signal (a travelling wave).

RULE 2. Whenever the activation signal covers the centre of a newly formed "cell" (at the shell edge), the whole "cell" is activated and becomes "black". If its centre is not covered, the "cell" stays "white".

Rules 3 and 4 govern the development and the interaction of pattern elements. They concern especially the "macro" level of interpretation.

RULE 3. Lines do never cross each other. When two lines meet, they terminate each other.

RULE 4. Lines may branch.

Let us first look at some details of Rules 1 and 2, controlling where "starting cells" are produced and which new "cells" can be activated.

The activation signal

In the "*Oliva* game", a starting "cell" at the shell edge is stimulated. Its centre then emits a short-duration activation signal, which keeps travelling. Fig. 3 shows the

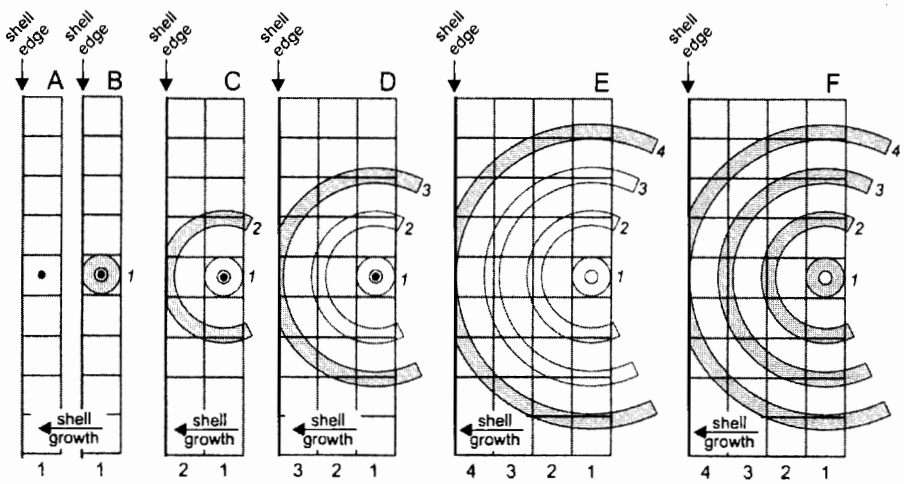

Figure 3. The "*Oliva* game": simplified representation of the activation signal. A: at time *t1*, a row of "cell" is formed (row 1, then at the lip edge). B: one of the newly formed "cells" emits a signal, which propagates as a travelling wave. C: at time *t2* a new row of "cells" (row 2, new shell edge) is formed. The signal wave is then at position 2 (the trace of the former position of the signal at time *ti* is shown in thin lines). The same process is repeated in D and E, at times *t3* and *t4*. F: Instead of showing all the successive stages of shell growth, the whole process can be conveniently represented in one single image, provided the signal wave is not too wide (the successive traces would then overlap).

successive stages of the propagation of such a signal. For facility, these successive stages can be represented in one single image, the square grid on which the "*Oliva* game" is played. It is the superposition of "frames" from the "movie" of shell growth.

Like moviemakers, we can measure time by counting how many frames separate two events. We can also measure speed by counting how many frames it takes to run a given distance on the grid.

The trace of the former position of the travelling signal on every "frame" can be kept in the final image as in Fig. 3F, provided the signal is not too wide, in which case the traces would overlap. The traces would then have to be drawn individually, on the final image.

The pattern left on the "shell" is the history (the movie) of what happened at the growing edge (as in Meinhardt's model). If only the first (newest) column of "cells" at the growing edge of the shell can be "painted", this has an important consequence: lines can never go "backwards" from newly formed cells to previously formed "old cells".

The travelling wave of the activation signal is characterised (see Fig. 4) by two parameters:

* a speed *Va* (expressed in units of shell growth rate, which was here above set at value 1). It is measured by the number of "cells" separating two consecutive traces at times *tn* and *tn+1*.

** a time of remanence *Rm* (expressed as the width of the wave, measured in units of "cell" dimension, also set here at 1). This makes sense because, at a given point on the "shell", the signal (a travelling wave, emitted as a short pulse) can stay active only during a given lapse of time.

There is no particular reason why *Va* and *Rm* should always keep a constant value). Each could for instance increase (or decrease) regularly as the shell grows. This can very much affect the aspect (and the history) of the signal, as illustrated in Fig. 5.

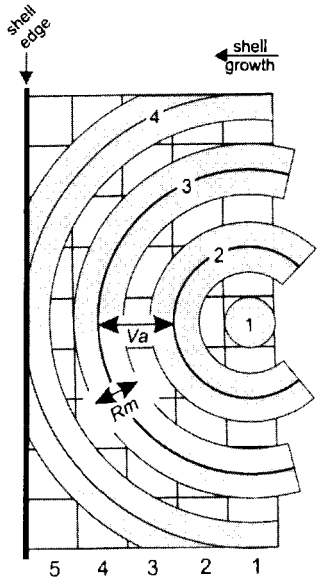

Figure 4. The "*Oliva* game": characteristics of the activation signal. The travelling wave has a speed *Va* (the distance between two successive positions at times tn and *tn+i*, see Fig. 3). It also has a width *Rm*. Both *Va* and *Rm* can be expressed in units of "cell" dimension, here taken to be 1. In this example, *Va* = 1.5, *Rm* = 1.

Reaction to the activation signal

It should be remembered (rule 2) that only newly formed "cells" (at the shell edge) can be activated. Only the portion of the signal that covers the "cells" at the shell edge can activate anything. The active portion of the signal is shown in dark grey in Fig. 6. In general, the wave *n* (at time *tn)* could have activated only the "cells" in row *n*.

If the centre of any "cell" in row *n* is touched by the activation signal at time *tn*, the "cell" is activated and becomes "black". If the signal does not touch the centre, the "cell" is not activated and stays "white". An example is given in Fig. 6b.

In some cases, it is not obvious whether the centre of a given "cell" (for instance, see the "cell" A-4) is covered or not by the signal. It is possible to use high-precision measurements, together with statistical error calculations. We rather suggest solving the problem by flipping a coin (or just guessing).

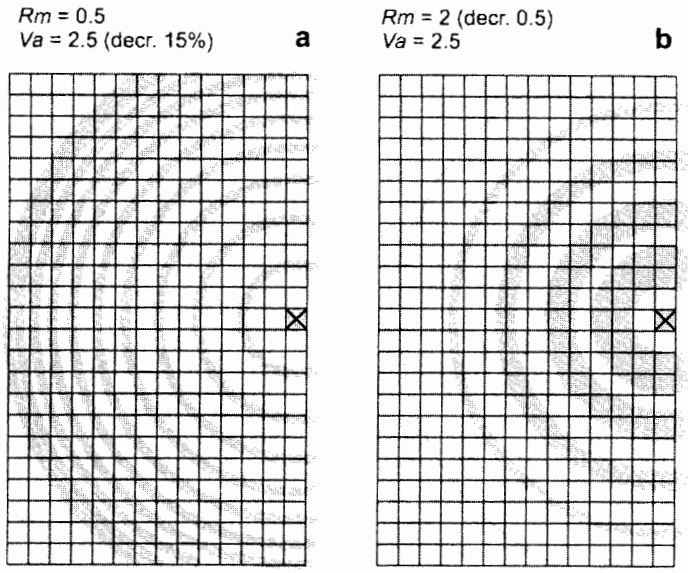

Figure 5. The "*Oliva* game": characteristics of the activation signal. The speed *Va* and the width *Rm* are not necessarily constant in time. Example a: *Rm* is kept constant at 0.5, while *Va* decreases geometrically (minus 15% at each time interval). Example b: *Va* is kept constant at 2.0, while *Rm* decreases linearly (minus 0.5 at each time interval).

The issue is not so important, especially if many "cells" are considered. Furthermore, little mistakes in applying the rules will give a more natural rendering of shell patterns (these are not so "perfect", when examined under magnification).

The image of a "central sensor" is not as outlandish as it may first seem. It is just a crude simulation of receptors that work under external control and only above a given threshold.

Simple pattern elements

Some examples (selected amongst a large number) will show what happens if one selects different sets of values for the characteristics *Va* and *Rm* of the activation signal. Any change in the values of these parameters results in the activation of different "cells", producing completely different patterns.

Fig. 7 gives some examples of patterns obtained with fixed values of *Va* and *Rm*.

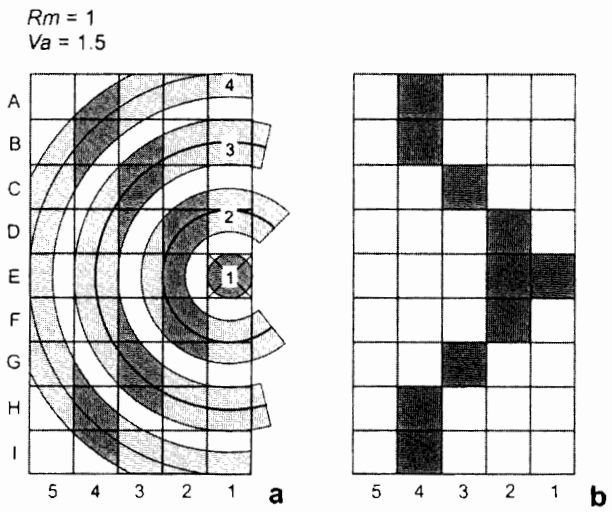

Figure 6. The "*Oliva* game": reaction to the activation signal. Here, $Va = 1.5$, $Rm = 1$.
a: The wave represented at time *t2* could activate only "cells" in row 2 ("active portion" in dark grey). In general, the wave represented at time *tn* could activate only "cells" in row *n*. If the centre of any "cell" in row *n* is covered by wave *n*, the entire "cell" becomes black. In case of doubt (like the "cell" A-4: is the centre covered or not?), follow the instructions in text.
b: outcome: pattern remaining after the construction elements (wave traces) are removed.

Fig. 8 gives some examples of patterns obtained by varying the values of either *Va* or *Rm*.

It should be noted that a regular decrease in *Rm* can result in spontaneous termination of the pattern (the wave becomes thinner and thinner, to the point of disappearing). The same result can be obtained by a regular decrease in *Va*. The progress of the wave becomes slower and slower, to the point where, at time tn, it does not reach the "cells" of column n anymore.

The chevron paradigm.

A chevron is here defined as a set of two lines diverging from a point (see Fig. 9). The angle of the chevron is bisected by the spiral direction at the point of origin. Chevrons invariably open towards the lip.

Many of the outcomes of the "*Oliva* game" are patterns (or fragments of patterns) actually observed on *Oliva* shells. Our game is probably more general than its nickname indicates, because one also obtains some patterns that are not found in the genus (for instance the open ocellus in Fig. 8 are not found in *Oliva* but present in *Cypraea*). Notice that all the patterns produced by the "*Oliva* game" are symmetrical and derive from a particular set of lines: the chevron.

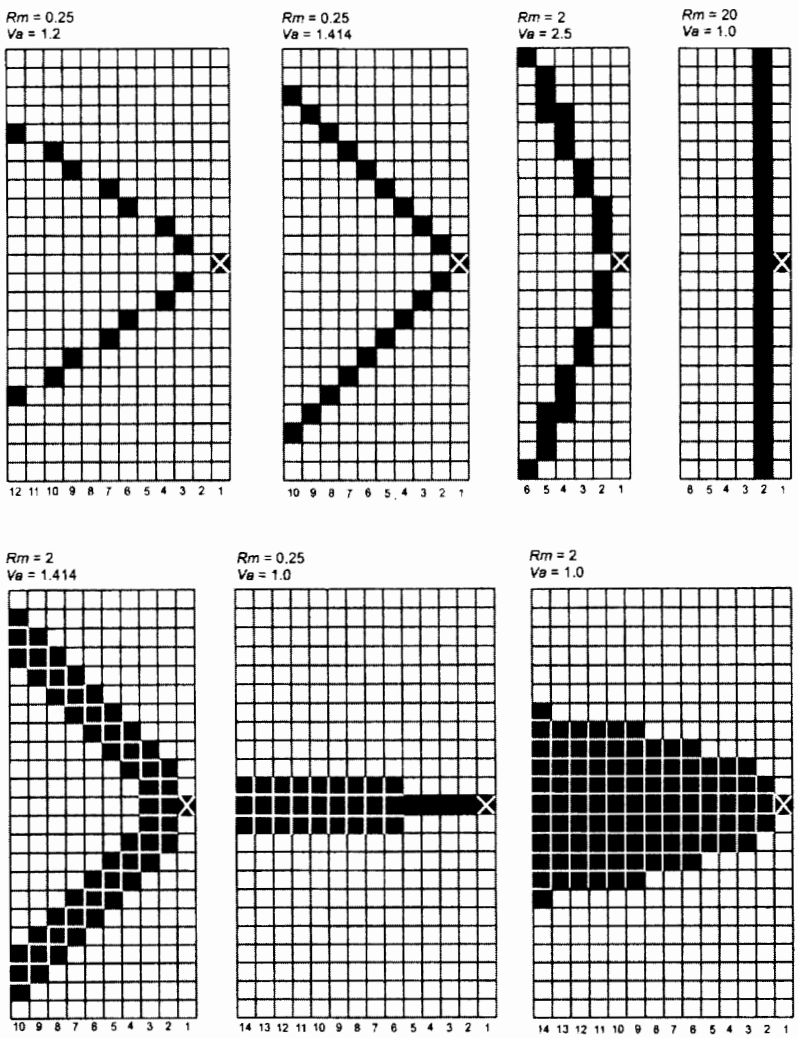

Figure 7. The "*Oliva* game": some examples of patterns obtained with fixed values of *Va* and *Rm*.

Conversely, nearly all (all?) the actual pattern elements observed on *Oliva* shells can be derived from chevrons. This "chevron paradigm" allows a reductionist (and hence workable) approach to the description of isolated pattern events in terms of comprehensible parameters. It could thus open the way to the analytical description of complex shell patterns.

Simple chevrons can be characterised (see Fig. 9) by the position (co-ordinates) of the origin, the opening angle, the length and the width of the branches (actual chevrons on shells are not necessarily symmetrical). The description of more complex chevron derivatives would involve their curvature and its mode of variation.

Changing the angle of the chevron (see Fig. 10) produces a continuous series of intergrades linking horizontal lines, chevrons and vertical lines. Varying the thickness and the curvature (see Fig. 11) produces a continuous series of intergrades linking simple chevrons, solid triangles, rounded chevrons and solid semi-ovals.

Understanding the development and the interaction of basic pattern elements requires the application of rules 3 and 4.

Mutual termination of lines

In the patterns of *Oliva* shells, lines never cross each other. Every time two lines meet,

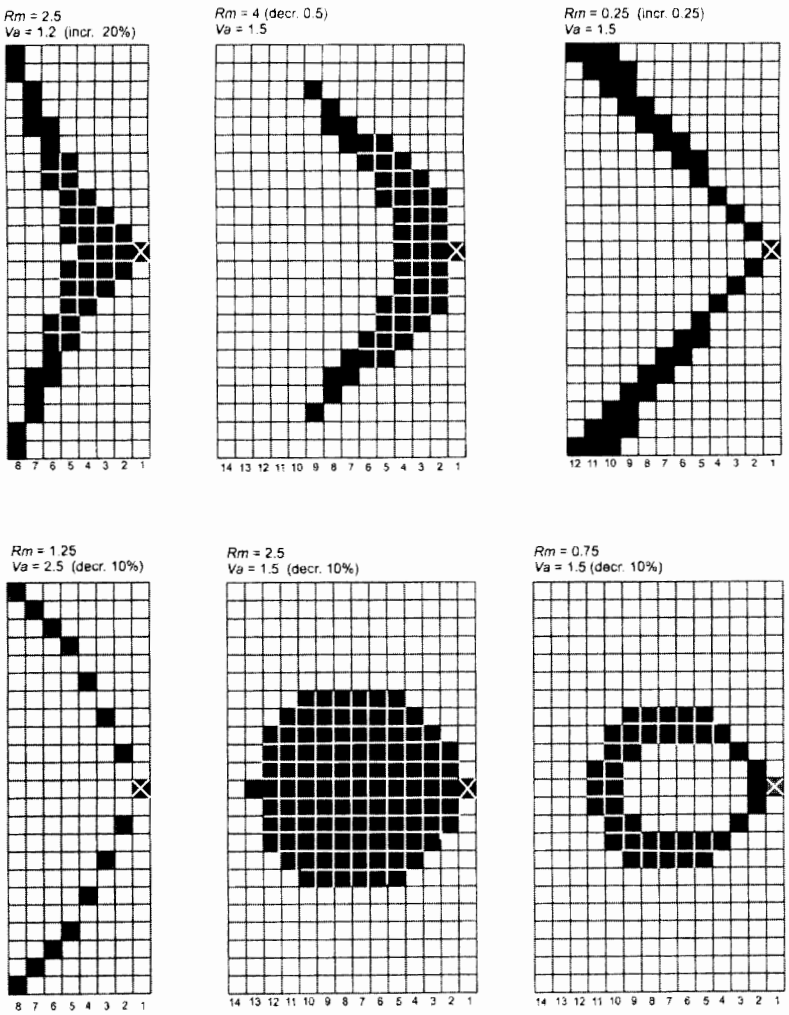

Figure 8. The *"Oliva* game": some examples of patterns obtained by varying the values of either *Va* or *Rm*.

both lines invariably stop (mutual termination of lines). In some cases (see Fig. 12), lines *appear* to cross each other. On close examination, however, this illusion is dispelled. The effect is due to the activation (induction?) of a new starting point, close to the point of mutual termination.

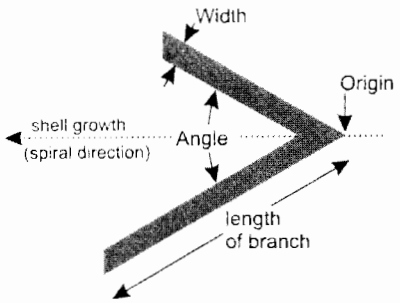

Figure 9. The simple chevron is bisected by the spiral growth direction of the shell. It can be characterised by the position of the origin, the opening angle, the length and the width of the branches.

Figure 10. The "chevron paradigm". Varying the angle of the chevron produces a continuous series of intergrades linking horizontal lines, chevrons and vertical lines.

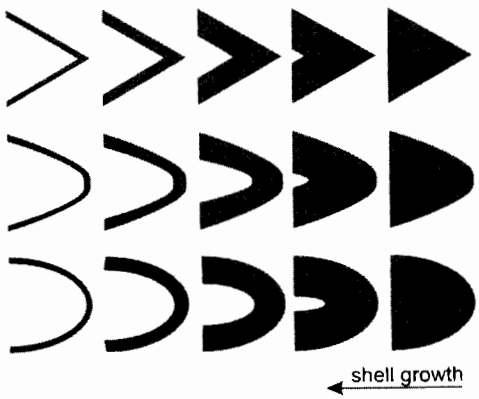

Figure 11. The "chevron paradigm". Varying the thickness and the curvature produces a continuous series of intergrades linking simple chevrons, solid triangles, rounded chevrons and solid semi-ovals.

As shown in Fig. 13, mutual termination of lines has a paramount simplifying effect on patterns. Without this phenomenon, shell colour patterns would be an inextricable maze of lines, ever increasing in complexity as the shell grows.

Branching

Branching lines are very frequently observed to start from regular chevrons. Actual start of the branching does of course begin when the "branching cell" is still at the growing edge of the shell.

Branches can grow only "inside" the chevron, never "outside" (otherwise, the line would grow "back", see Fig. 14). So, lines going "down" can only branch "up" and lines going "up" can only branch "down". In the case of straight chevrons, the angle of branching is the same as the starting angle of the chevron.

Branches arising directly from a chevron constitute "primary branching". Primary branches can also branch again ("secondary branching"), and so on (see Fig. 15). That figure also illustrates that branching has a considerable complexifying effect on pattern development.

Mutual terminations and branching have a profound influence on pattern development. These processes must of course be identified for pattern description and analysis.

ELEMENTARY PATTERN ANALYSIS

One proceeds by first determining a given area to be analysed. One could imagine working directly on the shell, but it is far easier to use a *camera lucida* drawing (or a photo, a Xerox or a direct scan of the shell). The direction of growth must be known.

One will quickly realise that some lines cannot be properly analysed because we have no data on their "history"; these are the imported patterns, originating from

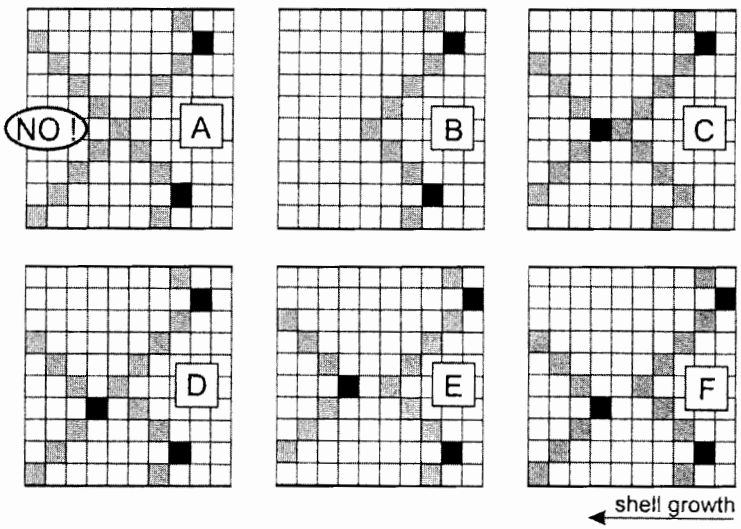

Figure 12. The "*Oliva* game": mutual termination of lines. Starting points of chevrons are shown in black. In actual *Oliva* patterns, lines appear never to cross each other as in A. When two lines meet, they do terminate each other as in B. Cases of apparent line crossing are due to situations like C, D, E or F.

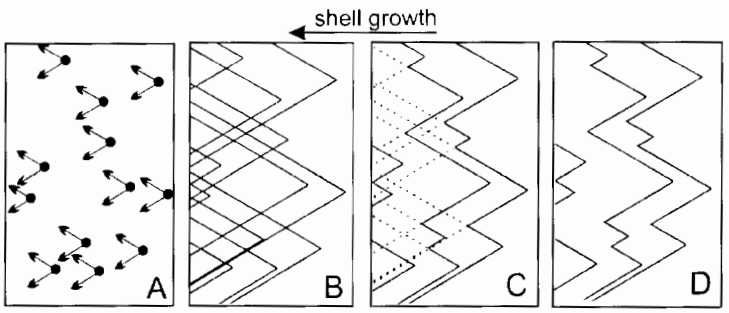

Figure 13. The "*Oliva* game". Effect of mutual termination of lines on pattern growth. A: chevrons grow from initial starting points. B: How the pattern would look without mutual termination of lines. C: many lines (dotted) result from crossings and are not allowed. D: Actual resulting pattern.

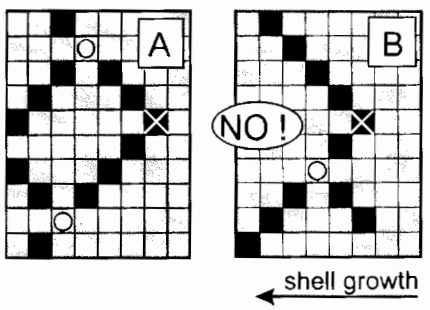

Figure 14. The "*Oliva* game": formation of branches. Schematic view, microscopic scale. Starting cell: black, branching cell: white circle. A: lines always branch "inside" the chevron. B: lines can not branch "outside" the chevron.

outside the selected area. In Fig. 16 imported patterns are marked with an arrow.

The other basic features are easily recognised (see Fig. 16): origins of chevrons spontaneous and mutual terminations of lines, primary and secondary branching. All can be conveniently marked with appropriate symbols. We need to have one more piece of information: the approximate angle of the chevrons.

Let us now test on actual examples if all this is only a dream or if it fits reality. In this short presentation, only the simple case of chevrons with constant angle will be considered.

Example: O. reticulata

Fig. 17A shows the shell and Figure 17B the portion to be studied. In Fig. 17C, the basic elements are identified. In the simple approach presented here we are looking only for chevron starts, branchings and sponta-

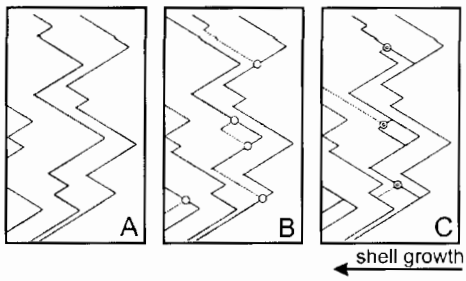

Figure 15. The "*Oliva* game": effect of branching on pattern growth. These three patterns originate from the same chevrons. A: no branching. B: primary branching (open circles). C: primary branching (open circles) and secondary branching (centred circles)

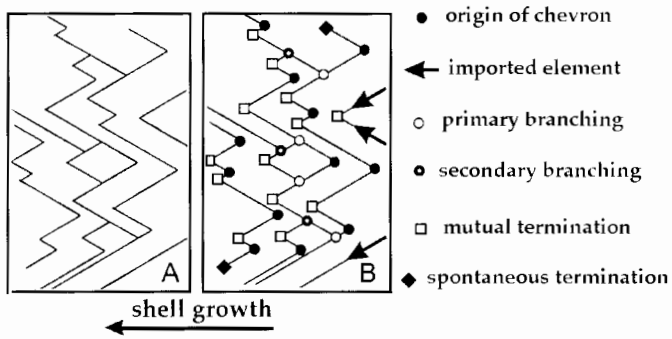

Figure 16. Pattern analysis: recognition of elements. The basic features of the pattern in A are individually identified in B.

neous ends. Imported patterns are also identified and marked. Note that we are completely neglecting the points of mutual terminations (they bring no information because they follow automatically from the starting points and the angle).

If one suppresses the actual pattern, one is left with Fig. 17D. If the analytical procedure was correct, then this figure should contain all the pattern descriptive points (the elements necessary to describe the pattern). That assumption can be easily tested by reconstructing the pattern, starting from Fig. 17D, starting from the origins, respecting the angles observed in Fig. 17B, respecting mutual terminations and stopping when spontaneous termination is required. The agreement between the resulting Fig. 17E and the original Fig. 17B is quite acceptable.

Quantitative pattern description. There were 24 starts, 10 spontaneous ends (42% of starts) and 1 branch (4% of starts).

Style analysis. One will notice that the spatial disposition of the starting points is far from random (see Fig. 17F). The "herringbone" pattern of this form does actually result from the regular arrangement of starting points into narrow spiral and axial zones (see Fig. 17F). The effect is very much enhanced by the near absence of branchings.

Example: O. vidua

The same analytical steps described for *O. vidua* in Fig. 17 are repeated for *O. porphyria* in Fig. 18

Quantitative pattern description. There were 37 starts, 0 spontaneous ends (0% of starts) and 51 branches (138% of starts).

Style analysis. This species is famous for its large, beautiful " tent pattern". We know immediately that these tents are not chevrons (they point in the wrong direction). One will notice that, as in the previous case, the spatial disposition of the starting points appears far from random (see Fig. 18F). This possibly explains the large "mesh" pattern but it does not explain the "tents". Examination of Fig. 18C shows that the large "tent" pattern is due to the grouping of many starting and branching points into narrow axial clusters. Nearly all the "tents" originate from at least one branching point.

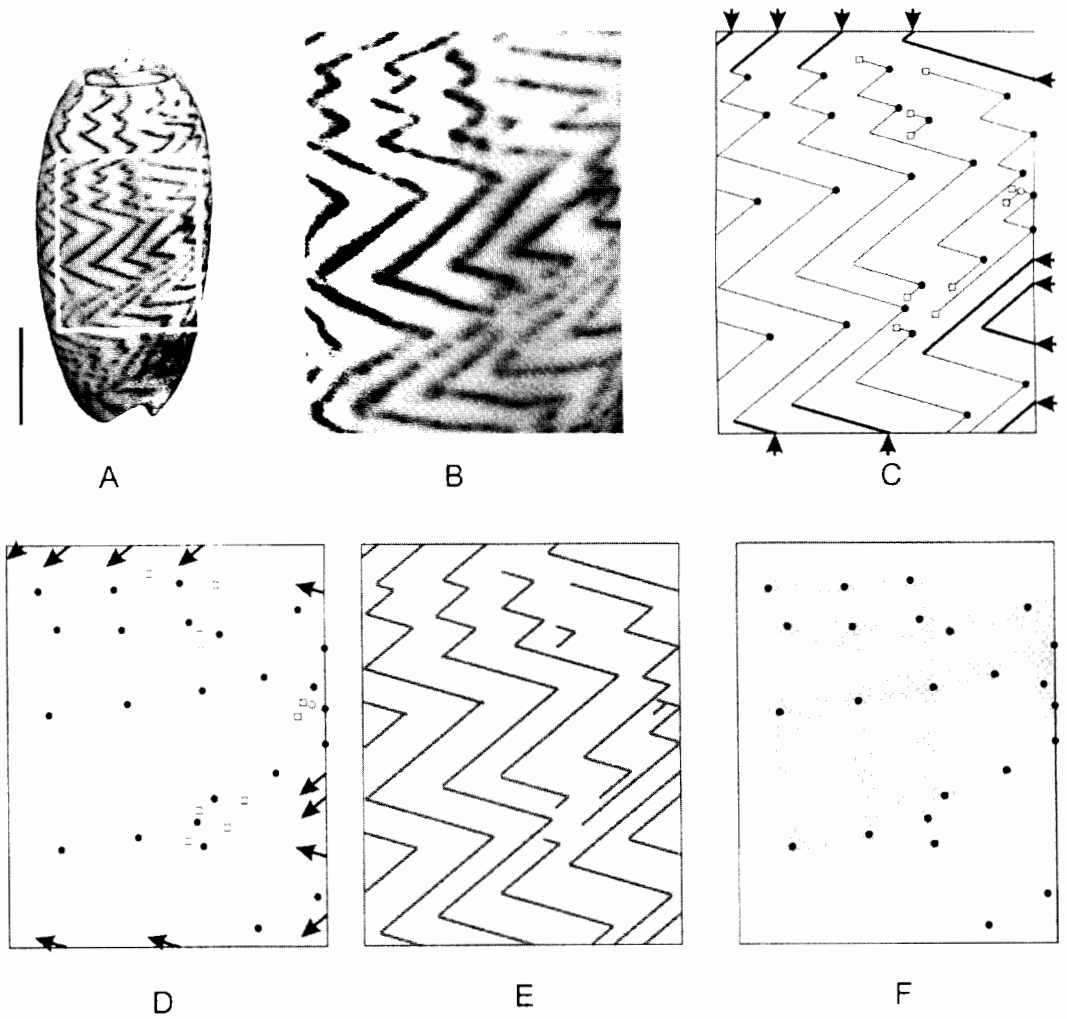

Figure 17. Analysis of actual shell patterns. A: Shell of *Oliva vidua* (Röding, 1798), Philippines, dorsal view. Scale bar: 10 mm. B: portion of pattern to be analysed. Note chevron angle about 55°. C: identification of pattern elements. Arrows: imported elements, black circles: starts; white circles: branchings; white squares: spontaneous terminations. D: pattern descriptive points. E. Test of fit: pattern reconstruction, starting from D (compare to B). F: "style" analysis (see text).

Taxonomic criteria?

Can such simple data on patterns be used for taxonomic purposes? The quantitative data found just above seem encouraging.

Let us, for the moment, be cautiously optimistic. We have not yet accounted for variability. So, the above example successfully separated two specimens (Table 1), not yet two species. Work along these lines is being pursued.

Table 1. Comparison of specimens of *Oliva vidua* (Fig.17) and *Oliva porphyria* (Fig. 18).

character	specimen of *O. vidua*	specimen of *O. porphyria*
chevron angle	55°	75°
spontaneous ends	42 % of starts	0 % of starts
branches	4 % of starts	138 % of starts

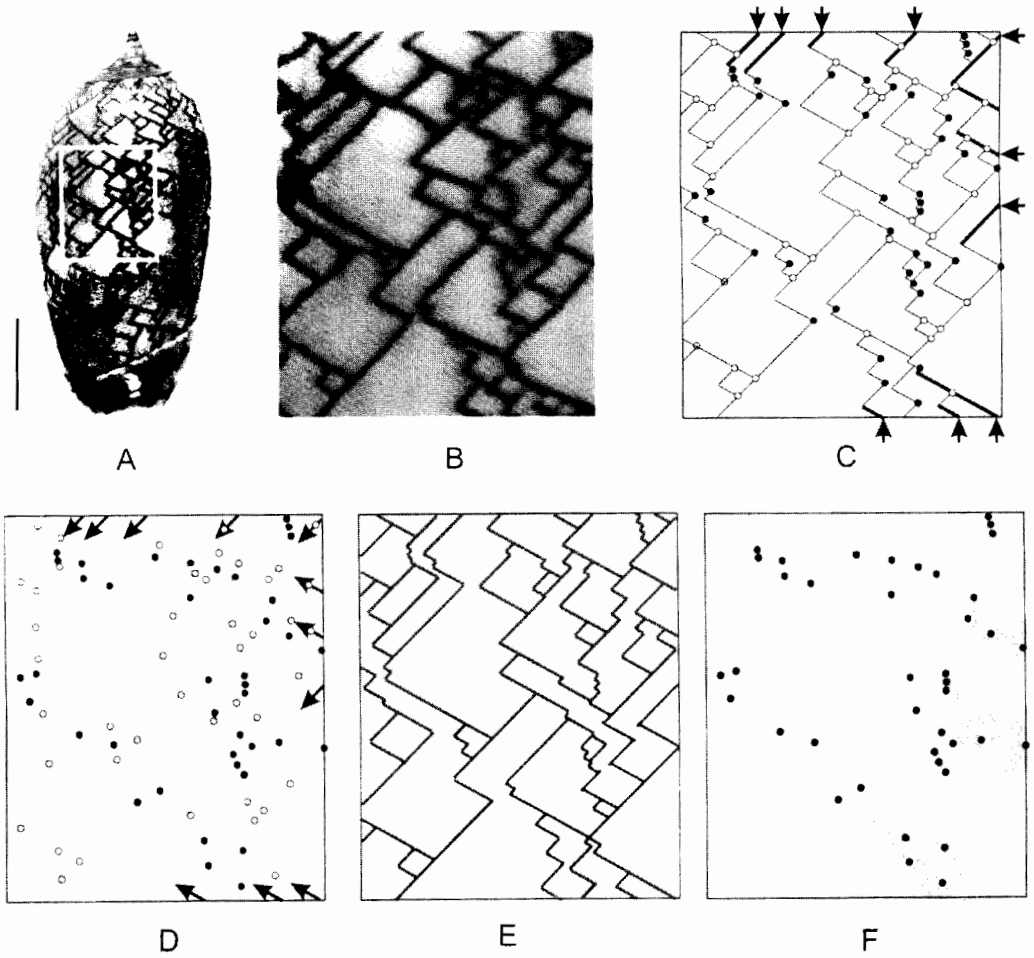

Figure 18. Analysis of actual shell patterns. A: Shell of *Oliva porphyria* (Röding, 1798), West Panama, dorsal view. Scale bar: 10 mm. B: portion of pattern to be analysed. Note chevron angle about **75°** C: identification of pattern elements. Arrows: imported elements, black circles: starts; white circles: branchings; white squares: spontaneous terminations. D: pattern descriptive points. E. Test of fit: pattern reconstruction, starting from D (compare to B). F: "style" analysis (see text).

REFERENCES

Greifeneder, D. 1981. What do we know about Olividae. Contributions to the study of Olividae. - Acta Conchyliorum 1:1-90.

Meinhardt, H. 1995. *The algorithmic beauty of sea shells.* Springer, Berlin.

Petuch, E.J. & D.M. Sargent. 1986. *Atlas of the living Olive shells of the world.* 253 pp., CERF editions, Charlottesville, VA. 235 pp.

Tursch, B. 1998. Taxonomic problems in the genus *Oliva*. - Phuket Marine Biological Center Special Publication 18(2): 263-284.

Tursch, B., J.M. Ouin & J. Bouillon. 1995. On the structure of a population of *Oliva oliva* (L., 1758) in Papua New Guinea (Studies on Olividae 22). - Apex 10(2/3): 29-38.

Tursch, B., D. Greifeneder & R. Duchamps. 1999. A long neglected problem: separating *Oliva vidua* (Röding, 1798) from *O. elegans* Lamarck, 1811. - *Phuket Marine Biological Center Special Publication* 19(2): 323-340.

Van Osselaer, C., J. Bouillon, J.M. Ouin & B. Tursch. 1993. Studies on Olividae XVIII. The distribution of *Oliva* species and the variation of their colour patterns in Hansa Bay (Papua New Guinea). - Apex 9(2/3): 29-46.