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I. Introduction

While looking over the collections of the Museum of Natural History of Berne, the author could not help being struck by the remarkable variety and often extreme complexity of the colour patterns of the Molluscan shells. It might even appear at first sight, that there is hardly any geometric or irregular design which is not represented on some specimen or other from these collections: squares, polygons, networks, checkerboards, labyrinths, bright, sharply delineated bands, zigzags, vague blotches, the variety appears endless and is certainly unsurpassed in the animal kingdom¹ — this in spite of the fact that most molluscan colour patterns are produced, so to say, from a single line and not from a complex surface, as are those of most other animals.

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

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

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

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

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

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

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

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

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

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

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

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

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