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at their extremities, and in the adult stages these blotches, aligned in more or less transverse rows, are all that may be left of the earlier zigzag pattern (Pl. IX, fig. 2).

VI. Relation between colouring and sculpture

The relationship between colouring and sculpture on the Molluscan shells is extremely variable, and at times quite complex: Wrigley's statement (1947, p. 212) that «colouring and sculpture are conformable» can only be considered as a very general approximation of the truth, even if one were to extend the term «conformable» to include any apparent influence whatever of the ribbing on the pattern elements: and indeed, in the cases where these latter are not parallel to the ribbing, this one will usually have to be pretty sharp or strongly developed to have any significant influence. A more accurate version of that «law» would read thus: Colouring appears generally to show some relation to sculpture, or to be in some degree influenced by it.

Even though the relationship between colouring and sculpture may at times be vague or doubtful, there are numbers of cases where the colour patterning appears entirely controlled by, or conformable to, the sculpture; and in other cases where such conformability is not immediately apparent, the first is impossible to explain without reference to the second. *Charonia tritonis* and *Harpa major* Röding were mentioned by Wrigley as good examples of close conformity between colouring and sculpture, and indeed appear to be so in the adult stages at least. The situation might at first sight seem different in *Pyramidella maculosa*: the colouring here comprises two transverse components, one of numerous brown bands, the other of scarcer, more irregular, wider, and rather indistinct bands that make an angle with the first. Fine white radial lines cut through the narrow bands and deeply incise the wide ones (Pl. IX, fig. 3). No ribbing could be observed in any of the individuals examined here, not even in the juvenile stages. A closer inspection, however, reveals the presence on the inside surface of the shell of periodic denticulated swellings such as are normally found under varices. The denticles of the swellings are often continued between these structures by radial interior ribs. It may then be observed that the white radial lines on the outside of the shell correspond to these denticles and interior ribs; and that the indistinct dark bands are laid down in front of (= distally from) each swelling and probably at about the same time, and are thus secreted far inside the shell. To have tried to «explain» or describe the outside colouring without reference to the sculpture would in this case have been senseless, even though here the sculpture is not visible on the outside of the shell.

It appears that there are at least four main types or categories of relationship between colouring and sculpture: these are essentially the same that had already been mentioned by the author in 1966 (p. 237) when discussing the positions of denticles relative to ribs. These categories may be briefly summarized as follows:

- (1) Independent type: Element 1 bears no evident relationship to element 2
- (2) Subordinate type: When element 1 vanishes, 2 disappears
- (3) Associated type: When element 1 vanishes, 2 remains unaltered
- (4) Correlated type ⁴⁷: When element 1 vanishes, 2 changes.

In all the cases studied, element 1, or the primary element, was taken to be the sculpture (esp. the external ribs), as it seems to influence the pattern or elements thereof, without being influenced by it, and also appears in general more stable than the pattern.

(1) Independent type. This type includes almost all the colour patterns and pattern elements which are not oriented as the sculpture, and some with the same orientation. It appears evident that though the outline of the white transverse zigzags of *Columbella fulgurans* Lam. may be influenced locally and in a minor degree by the radial ribbing, these pattern features as such are quite independent of that ribbing; the same applies to the radial rows of spots in *Mitra mitra* L. and the radial bands of *Terebra subulata* Lam., whose limits do not correspond to those of the radial sculpture elements.

In many cases, one has a pattern to all appearance independent of the ribbing in regard to its origin and general aspect, and yet as indicated above for *Columbella fulgurans* Lam., clearly influenced by that ribbing. This influence may affect the shape and/or shade of the colour patterns. In *C. fulgurans* local jags (embayments and projections) in the zigzags are seen to coincide with the ribs and interspaces of the radial sculpture (Pl. IX, fig. 4). These jags do not follow the trends of the growth lines, so it is clear that the influence there is that of the ribbing itself.

Another ribbing effect is the differential shading that it often produces in the patterns that traverse it. A good example of this phenomenon is seen in many individuals of *Arca zebra* Swains., where the chevron-shaped stripes are darker on the ribs than in the interspaces; a probably similar factor is operative in *Conus striatus* L. though there the denticles and indentations are usually better developed than the outside ribbing and may be mostly responsible for the light and dark stripes on the irregular transverse bands.

(2) Subordinate type. Here the very presence of the secondary element seems to depend on that of the primary, though the reverse does not appear to be true. The most striking examples of subordinate elements are the various features of a varix which appear to exist only in the presence of the varix itself: thus the rows of spines of *Murex tenuispina* Lam., the dark radial stripes on the varices of *Harpa nobilis* Lam., the dark colouring in front of the «internal varices» of *Pyramidella maculosa* Lam., etc. In all these cases, the secondary element could theoretically be lacking (and in the last named species appears occasionally so to be ⁴⁸. There is a special sort of subordination which could be termed «necessary

⁴⁷ The elements termed here «correlated» were called «dependent» in the author's 1966 work. That latter term, however, has already had prior usage in the German «school» of conchology (see NEUMANN, p. 405: abhängig), to designate a quite different type of phenomenon, and is thus here discarded.

⁴⁸ The «subordinate» phenomenon shows some similarity to that of «influence» (see above paragr.) and there might be cases where it would be hard to establish which one one had. In general «influence» is here considered as a secondary phenomenon in interelemental rela-

subordination», e. g., the relationship in *Natica* of funicle to umbilicus: if there were no umbilicus there could be no funicle!

(3) Associated type. When the primary element with which the secondary is associated positionally and otherwise, vanishes, or loses direct contact with it, the secondary maintains itself as if the primary element were still there. Here are to be included most of the radial lines and bands associated with ribbing of the same trend, which maintain themselves in the same position on the whorl face, whether this ribbing be present only in the juvenile stages and later vanishes, or whether it remains throughout shell growth. Examples worth citing might include the white radial lines of *Harpa major* Röding, the dark lines of *Alectrion glans* L., *Fasciolaria hunteria* Perry, etc. It might be added that a distinction between this type of element and the next is generally made possible only through disappearance of the primary element (ribbing mostly), on observing how the secondary element is affected; such a distinction is thus difficult to achieve in wholly ribbed shells, except by analogy with other similar shells and elements.

A remarkable example of association is that of warts with ocelli in *Neritina squamosa* Sowb. (Pl. IX, fig. 6). Many specimens of that species, and even more of related species of *Neritina*, such as *N. pulchella* Recl., have ocelli with lobate distal rims, the latter often with peculiar eyelash-like extensions (Pl. IX, fig. 5); these ocelli have a somewhat irregular crossed-oblique distribution (see p. 22). In most *N. squamosa* Sowb. available, a wart appears under each ocellus, with the rim usually to be found somewhere on the wart-slope (Pl. IX, fig. 6). Often the oblique and transverse alignments of the ocelli are emphasized by ridges: on such ridges the warts may be poorly developed or even absent. The ridge pattern may in places have an appearance rather strikingly like that of the partly reticulated zigzags on some *Strombus vittatus* L., illustrating once again the evident kinship of the crossed-oblique distribution and the rhombic network patterns. The «associate» relationship of warts and ocelli is demonstrated by the fact that the first may appear fully developed on homogeneously coloured shells and the second will remain fully developed and unmodified even on parts of the whorls where warts are lacking. The present wart-ocellus relationship is interesting in that it indicates that this associate relationship is not limited to radial elements.

(4) Correlated type. This type of element was the one termed «dependent» in the author's 1966 paper. Its essential character, in so far as can be ascertained, is that while the primary element and it are both present, it will, in its typical form maintain a very stable position in relation to the primary element, and indeed generally also to the shell as a whole ⁴⁹. As soon however as the primary element

tionships, as in elements independent of ribbing in origin, orientation, etc, yet being secondarily influenced by it. Subordinate elements to all evidence can exist only in association with ribbing, etc.

⁴⁹ This effect, at least apparent, of the primary element on the correlated element, recalls the phenomenon of influence: influence, however, typically affects elements not otherwise connected to the «source» of influence.

disappears or loses its connection with the correlated element, this latter one will tend to become modified, to shift its position, etc. often in a highly irregular manner.

In effect, thus, it looks as if the association of subordinate and primary element were generally total, and often necessary; that of the associate element complete in respect to position, while in the case of the correlated element, there appears to be fundamentally only a very approximate and general correspondance in position with the primary element, and evidently only some influence of the latter, direct or indirect, makes it appear as if this correspondance were much closer. It could be that the essential difference between associated and correlated element is simply the greater stability of the former, but with the limited amount of evidence at hand this appears impossible to assert.

An excellent example of correlated type of pattern elements may be found in *Pusia tricolor* Gm. (Pl. IX, fig. 7; Pl. XI, fig. 11). In the juvenile stages of that species, the transverse ribs are white (or rather are overlain by white bands), and the interspaces brown. A radial white stripe transects both bands and ribbing, connecting the transverse white bands with each other. As the ribbing grows fainter and finally vanishes altogether in the adult shell, the white transverse bands become more and more irregular, may extend into the brown bands to the point of splitting them into islands, this whole zone of alternate white and brown bands showing a most confused and complex pattern (Pl. IX, fig. 7, last whorl). The transverse white bands are of course here the correlated element, the radial white stripe a stable element unrelated to any sculpture and maintaining itself unchanged in the adult stages. — It may be added that here the frequency of occurrence of the white and brown transverse bands is less variable than their shape.

Another example shows both correlated and associated elements in a single pattern, and the way both these elements evolve: the juvenile *Fasciolaria hunteria* Per. shows white transverse swellings and brown radial grooves. In the adult both swellings and grooves vanish, but the white transverse areas have multiplied, and become completely irregular, while the brown radial lines originally in the grooves maintain unchanged their original aspect and position on the whorl.

In the following examples, associated and correlated elements do not appear together, but one after the other: in the first case correlated elements appear first; in the second, presumably correlated elements show up last.

In *Mitra papalis* L. the juvenile stages show transverse swellings on the distal side of growth interruptions. These swellings are here white, the rest of the whorl (at least above the suture) red with a few transverse white bands in addition to those on the swellings⁵⁰. Radial ribs are present but are not coloured differently from the rest of the whorl. What is seen therefore at this stage, is a pattern of transverse white bands irregularly correlated with similarly oriented swellings. In the adult, the red colour disappears, except on the ribs, where it persists as rows of

⁵⁰ There are thus at least two types of irregular combinations: one in which the secondary element is to be found with the primary only part of the time, the other in which the secondary is always found with the primary, but also outside of it.

spots conformable to those ribs. The swellings also vanish and the white transverse bands become indistinguishable from the white ground of the shell. In the adult stage of this species therefore we end up simply with a pattern of radial rows of red spots associated with the ribs.

In most *Planaxis lineatus* Costa, the brown bands on top of the radial ribs of the juvenile form persist unchanged in the ribless adult, and are therefore typical «associated» elements. In a certain fraction of individuals however, this pattern is present only in the young: in the adult, generally following on what appears to be a break in the shell, a completely different pattern is produced, consisting of very irregular and multitudinous radial lines and stripes (Pl. XI, fig. 10); only at the very bottom of the whorls, where the ribbing persists, do the lines, conformable with it, show some regularity. A preliminary conclusion would be that in such shells, an accident produced an alternation of colour pattern, and that this new pattern appears to be of the correlated type. It must be added that in rare shells the typical associated pattern does not appear, only the supposedly correlated one; and this one only in the later growth stages of the shell.

In some shells we have what might be called irregularly correlated elements. In *Rissoa grossa* Mich. and *R. lineolata* Mich., the elements in question, transverse brown lines, run down the interspaces of a transverse ribbing (Pl. IX, fig. 8): sometimes these lines are sinuous even within the interspaces, occasionally so much so, that the curves may extend onto the ribs: often too, the periodicity of the lines is different from that of the ribs, and we may have two lines per interspace, one on each side thereof: we thus see here no perfect conformity of lines and ribbing. — At about the middle of the whorl, where the ribs end, the lines usually become much more irregular and sinuous and either change markedly in direction, or shift strongly only to pursue later a course more or less similar to that followed in the upper part of the whorl (Pl. IX, fig. 8), or both shift and change direction. It is as if the presence of the ribs tended to confine or channel the lines along the interspaces in a course parallel to the ribbing, and only the absence of ribbing on the lower portions of the whorl allowed the lines to run their natural course. A clear example of this apparent dependence of the lines on the ribbing may be observed where the lines are more numerous than the ribs and are channeled in the interspaces two by two (Pl. IX, fig. 8): where the ribs end, these lines become unpaired and become all more or less (though very irregularly) equidistant. It may be added that in partly or wholly smooth varieties of these species the lines are generally more irregularly distributed and oriented than in the ribbed varieties.

In some cases, we have a phenomenon which might be termed «secondary correlation». In *Busycon contrarium* Conrad, concentric bands appear at or near the shell surface just proximal to growth breaks (Pl. IX, fig. 10). These bands, which occur only with breaks, may be considered as «subordinate» shell features. The relationship of the shoulder nodes to the breaks is less constant, and might be termed «irregularly correlated»: most often nevertheless, nodes appear at the

level of the growth breaks ⁵¹. The secondary correlation involved is that between bands and nodes: the first will usually cover the last, evidently not because they are directly related to them, but because both are related to the growth breaks.

VII. Interrelationships between pattern elements

Since the author hopes to be able to give a more extended consideration to that subject in the near future, only a few preliminary remarks will be made here.

The various types of relationship mentioned above as existing between pattern elements and ribbing seem to be present also in the interrelationships between the pattern elements themselves: they are here however often harder to elucidate, owing to the frequent absence of clearly defined «primary» features. Examples of various relationships are given below:

In *Conus generalis* L., when the radial homogeneous bands are well developed, they appear to be quite independent of the transverse sinuous lines.

Presence of «necessarily subordinate» elements is demonstrated by the relationship between cells and frame in networks; more typical cases of subordinate relationship could not be detected anywhere with absolute certainty; and indeed in the usual absence of clearly defined primary elements in shell patterns, such subordinate elements must be rare indeed.

In *Smaragdia viridis* L., black sinuous transverse lines are generally followed by rows of white blotches, often in a very conformable manner (Pl. IX, fig. 9). Yet each of these types of elements may be absent from one to many periodic cycles without the other being noticeably modified thereby. We have thus here to all evidence an associated type of relationship between black lines and white blotches; on account of the variable appearance of the elements, it might be termed an «irregular association». To note, however, that though the author has examined many shells of that species that showed only blotches (esp. in the Caribbean variety *viridimaris* Maury), he has never yet observed a shell with lines only: this, plus the very peculiar configuration of the black lines half-surrounding the white blotches, gives the impression that the latter may be the dominant factor in the colour pattern.

A somewhat similar relationship between elements seems to obtain in the case of some «junction figures». In the complex pattern figures of *Bulimulus coturnix* Sowb., *Neopetraeus arboriferus* Pil., etc. (Pl. V, figs. 9, 10) the relationship of the various parts to each other is always the same, even though the figures

⁵¹ The periodicity of appearance of labra is very irregular, that of the nodes much less so. When appearance of a new labrum is very much delayed, a node may be secreted before this new labrum appears, in addition to or in place of the adlabral node; or this interlabral node may continue to be secreted until this labrum finally appears, forming a very elongate node indeed! — see Pl. IX, fig. 10.