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Disturbance rings and shell shape in the Triassic brachiopod *Coenothyris vulgaris*

By

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With 12 figures in the text

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Abstract: *Coenothyris vulgaris* (VON SCHLOTHEIM) shows a correlation between the number of disturbance rings occurring on the shell resulting from environmental disturbance, and the shell shape. Increase in the number of disturbance rings is associated with a decreasing length/thickness ratio, and an increasing lenght/width ratio of the shell. Similar differences between Lower and Upper Muschelkalk populations are probably caused by evolutionary transformation rather than environmental modification.

Zusammenfassung: Bei *Coenothyris vulgaris* des unteren Muschelkalks werden die feinen Anwachslinien häufig von Stör-Ringen überlagert. Diese sind vermutlich Umwelt-bedingt (Stürme) und treten in jugendlichen Gehäuseteilen wesentlich seltener auf als in dem langsamer wachsenden Adult-Stadium. Da sich die Expansionsrate nach jeder Wachstums-Unterbrechung verringert, sind Gehäuse mit Stör-Ringen relativ schmäler und dicker als glatte Gehäuse derselben Population. Eine solche Beziehung gilt auch für Populationen des Oberen Muschelkalks. Sie wird jedoch überlagert durch eine evolutive Transformation in derselben Richtung, d. h. die Gehäuse werden insgesamt schlanker und höher gewölbt als im Unteren Muschelkalk.

Introduction

The aim of the present paper is to demonstrate the influence of environmental events on brachiopod shell morphology. The problem will be exemplified by the Triassic brachiopod species *Coenothyris vulgaris* (VON SCHLOTHEIM), a representative of the family Dielasmatidae SCHUCHERT, 1913, order Terebratulida. The investigated specimens (Fig. 1) come from the Terebratula Beds of ASSMANN (1944) in the Lower Muschelkalk from Strzelce Opolskie (Silesia, southern Poland), from the Lima striata Beds of SENKOWICZOWA (1957) in the Lower Muschelkalk from Wolica (Holy Cross Mountains, southern Poland), from the Upper Muschelkalk of Jarugi (Holy

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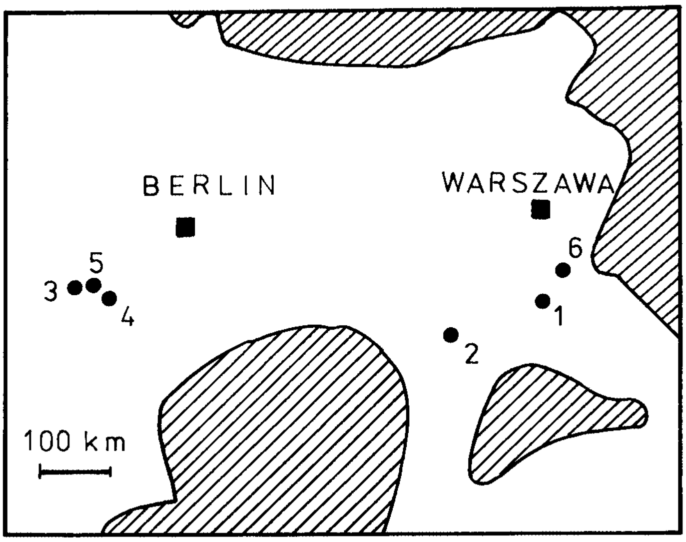

Fig. 1. Eastern part of the „germanotype" Muschelkalk basin with localities that yielded the investigated *Coenthothyris vulgaris*.
1: Wolica; 2: Strzelce Opolskie; 3: Reckenbühl; 4: Döllstedter Trift; 5: Marolterode; 6: Jarugi.

Cross Mountains, southern Poland), and from the Upper Muschelkalk of East Germany (Thuringia from Reckenbühl, Döllstedter Trift and Marolterode, see MÜLLER 1950).

Coenothyris vulgaris from the Muschelkalk

This species is well known from the Middle Triassic of numerous regions of Europe (see PÁLFY 1992, HAGDORN & SIMON 1993). It occurs also in the Lower and Upper Muschelkalk of Poland and Germany. Since long it has been recognized (SCHMIDT 1928 for example) that *C. vulgaris* from the Muschelkalk displays strong morphological variation. HAGDORN & SIMON (1993) have even speculated that differences between populations of this brachiopod from the Lower and Upper Muschelkalk might in fact justify distinction at the species level. Our material also shows clear morphological differences between the two levels. Populations from the Lower Muschelkalk contain thicker and more elongated forms than the ones from the Upper Muschelkalk, where flatter and more rounded forms predominate (Figs. 2, 3, 4). As a measure of relative thickness of the shell we used the lengh/thickness ratio (L/T), while the lenght/width (L/W) ratio has been used as a measure of relative elongation. The average value of the L/T ratio of populations from the Lower Muschelkalk is always smaller than in populations from the Upper Muschelkalk, while the

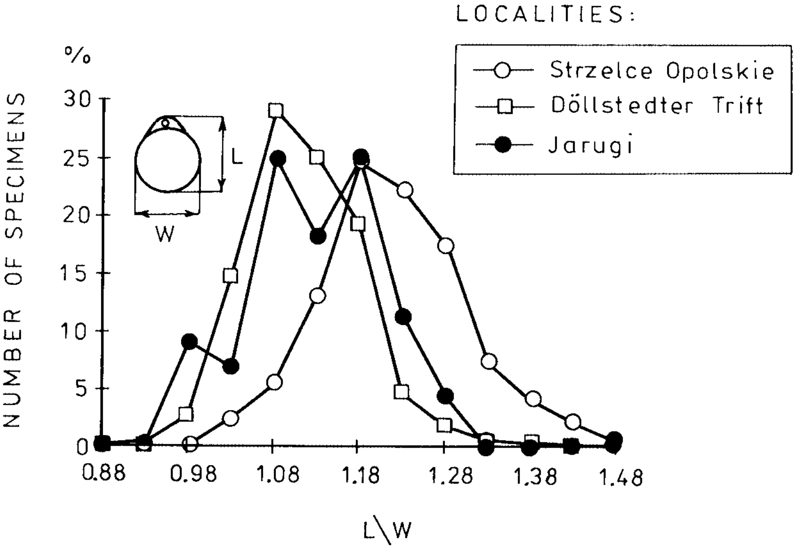

Fig. 2. Frequency distribution of L/W ratios in samples from the Lower (Strzelce Opolskie) and Upper (Döllstedter Trift and Jarugi) Muschelkalk populations of *C. vulgaris*. Data for Döllstedter Trift after MÜLLER (1950).

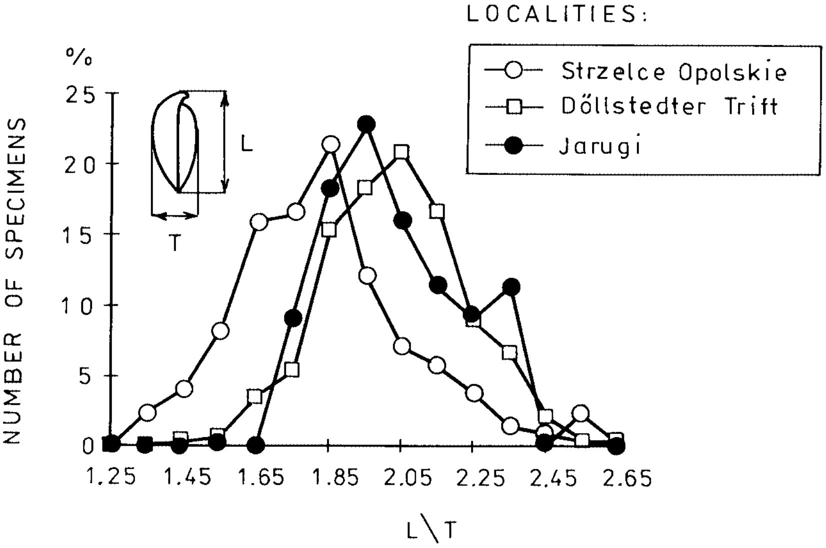

Fig. 3. Frequency distribution of L/T ratio of the shell in samples from the Lower (Strzelce Opolskie) and Upper (Döllstedter Trift and Jarugi) Muschelkalk populations of *C. vulgaris*. Data for Döllstedter Trift after MÜLLER (1950).

average L/W ratio for populations from the Lower Muschelkalk is always higher than in the Upper Muschelkalk (Figs. 2-4).

During this study it has been found that external differences are accompanied by internal ones: shells from the Lower Muschelkalk usually have upwardly directed hinge plates forming a more or less V-shaped structure, while hinge plates in the Upper Muschelkalk are running more horizontally and form a T-shaped structure (Fig. 4).

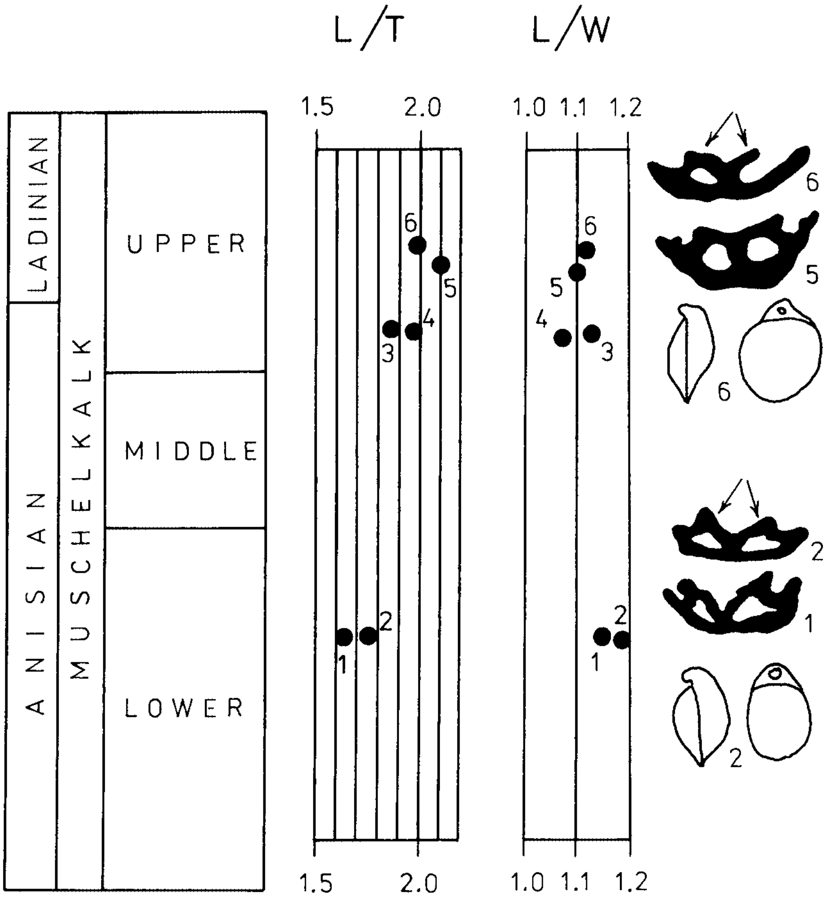

Fig. 4. Mean values of L/W and L/T ratios for populations of *C. vulgaris* from the Lower and Upper Muschelkalk from different localities; the type of hinge plate structures (arrows) is also shown in selected specimens. For locality numbers see Figure 1. Data for localities 3-5 after Müller (1950).

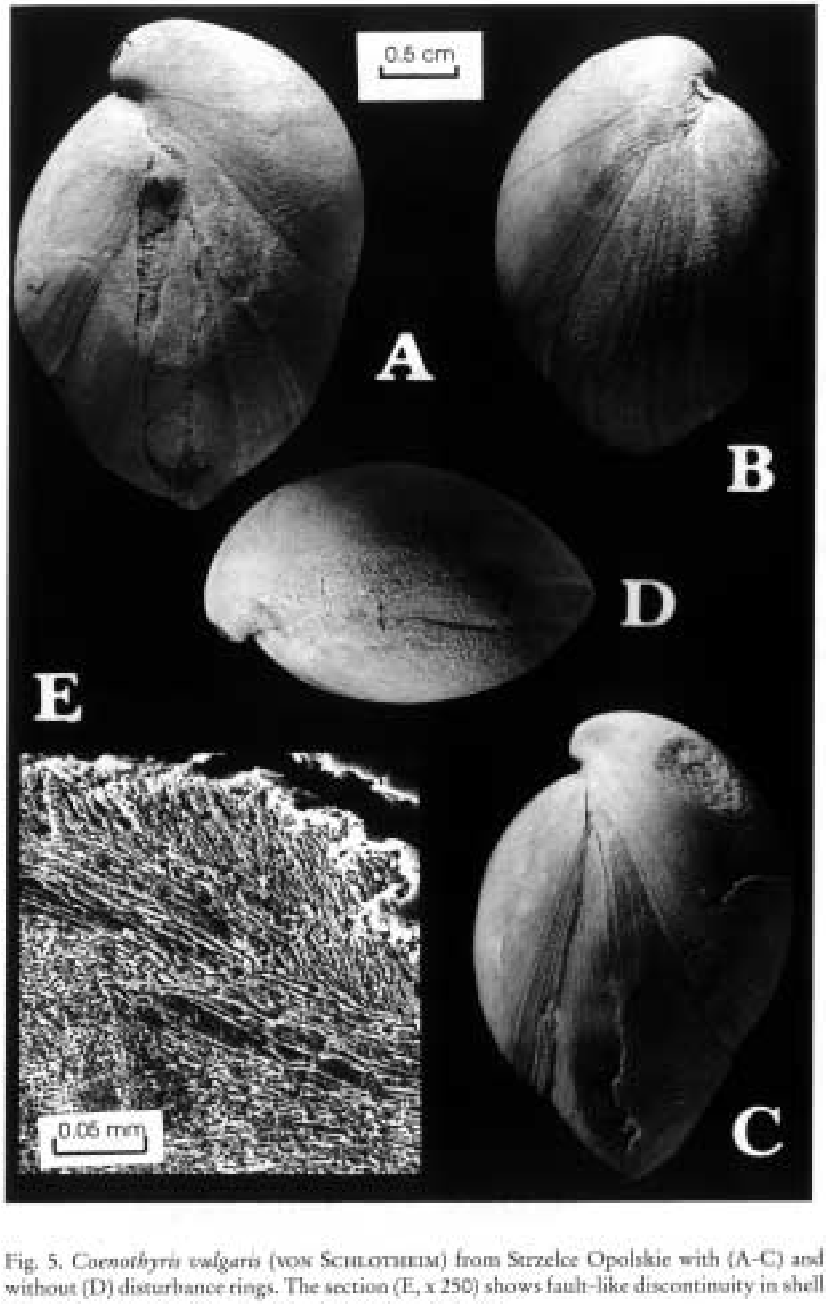

Fig. 5. *Coenothyris vulgaris* (VON SCHLOTHEIM) from Strzelce Opolskie with (A-C) and without (D) disturbance rings. The section (E, x 250) shows fault-like discontinuity in shell structure corresponding to a disturbance ring. A-D x 2.

Disturbance rings

Some specimens of *C. vulgaris* from Strzelce Opolskie, and Reckenbühl and Döllstedter Trift (see Müller 1950) have 'apart from ordinary and very fine growth lines, a different kind of very strongly expressed growth rings (Figs. 5A-C). About 16% of the specimens in sample No. 2 from Strzelce Opolskie display such rings (Fig. 6). Over half of them have only one ring, while

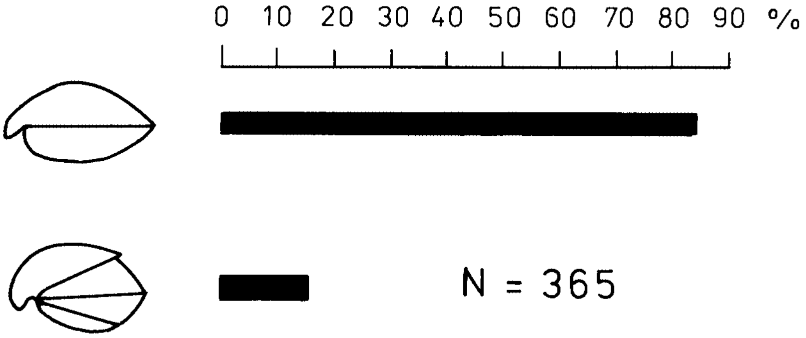

Fig. 6. Percentage of shells with and without disturbance rings in a population of *C. vulgaris* from Strzelce Opolskie (sample 2).

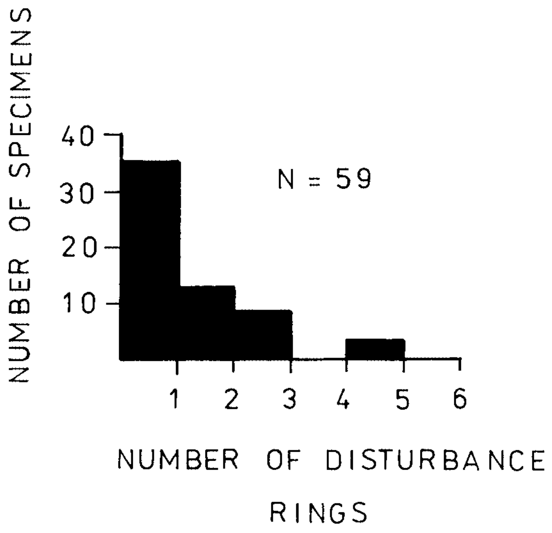

Fig. 7. Frequency of shells with various numbers of disturbance rings (sample Strzelce Opolskie 2).

specimens with more rings are less common (Fig. 7). This is a matter of probability, but it also suggests that a brachiopod having suffered more than more one such disturbance had a reduced chance to survive.

These growth rings are not randomly distributed over the shell. In most cases they are situated in the adult portion of the shell, while their number decreases toward the juvenile part of the shell (Fig. 8). As the growth rate is approximately 3 times higher in the juvenile than in the adult shell (THAYER 1977, ROSENBERG, HUGHES & TKACHUCK 1988), the adult portion of the shell reflects a time period three times as long as a juvenile portion of equal length. Consequently (Fig. 8), the number of the growth rings in the adult parts of the shells is nearly three times as high in the adult as in the juvenile parts! This suggests that the probability of a prominent growth break to occur is proportional to age of the brachiopod. On the other hand the statistical data (Figs. 6-8) indicate that the discontinuities were caused by random events. This view is corroborated by the shell microstructure. Thin sections (Fig. 5E) show that we deal with disturbance rings, sensu HILLER (1988; see also VOGEL 1959, WILLIAMS 1971): they are always associated with fault-like dislocations in the shell structure. Disturbance rings reflect random, temporary and abrupt changes in the environment. They injure the mantle, which in response refracts

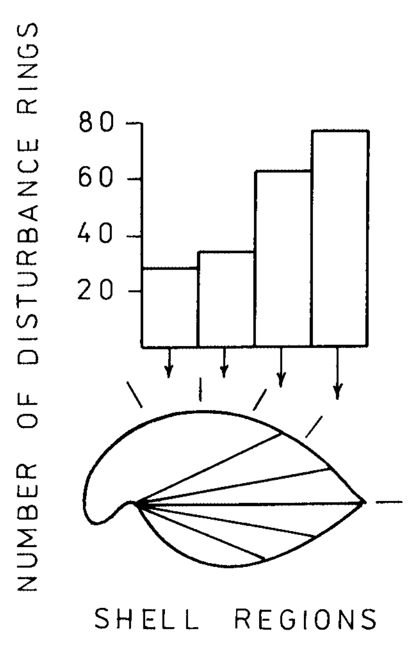

Fig. 8. Frequency distribution of disturbance rings in various shell regions measured on 68 shells (sample Strzelce Opolskie 1).

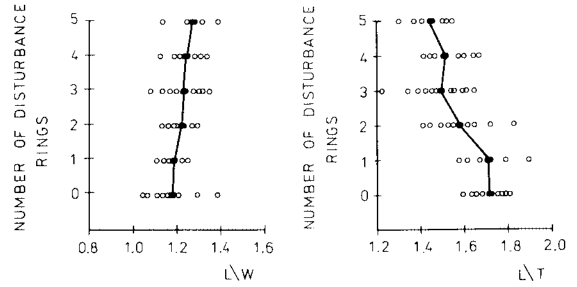

Fig. 9. Number of disturbance rings in relation to the average L/W and L/T ratios in shells of *C. vulgaris* from Strzelce Opolskie (sample no 1).

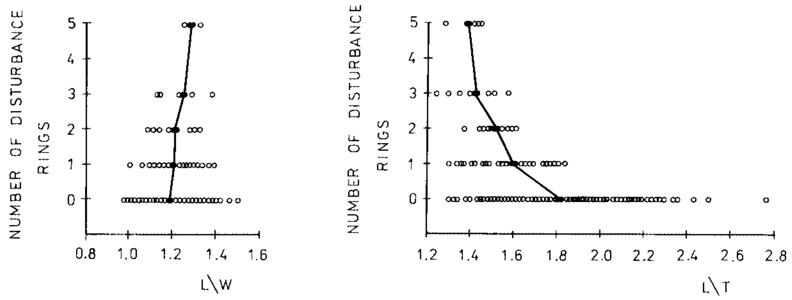

Fig. 10. Number of disturbance rings in relation to average values of L/W and L/T ratios in the shell of C. vulgaris from Strzelce Opolskie (sample no 2).

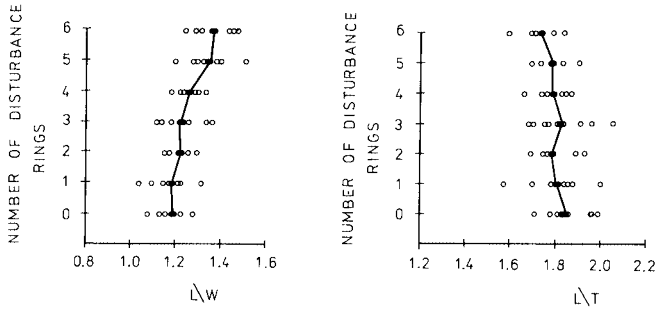

Fig. 11. Number of disturbance rings in relation to average L/W and L/T ratios in shells of the Cretaceous terebratulid *Concinnithyris* sp. from Annopol on the Vistula (Poland).

sharply inwards or regresses (Hiller 1988). After the disturbance, shell accretion recommences from the new position of the mantle edge (Williams 1971, Hiller 1988). As suggested by sedimentological data (Dzulyński & Kubicz 1975), the events responsible for the disturbance rings at Strzelce Opolskie (Figs. 5-8) were most probably storms. If this is true, the percentage of specimens with disturbance rings in various populations of *C. vulgaris* may serve as measure for the hydrodynamic energy of the environment in the particular area or horizon.

Disturbance rings and shell shape

During our studies we have found a clear correlation between numbers of disturbance rings and shell shapes (Figs.9-10). Shells that have more disturbance rings are thicker and longer, i. e. an increase in the number of disturbance rings leads to a decrease in the lenght/thickness (L/T) ratio, while the lenght/width (L/W) ratio increases. This rule applies also to other terebratulid brachiopods. The same relationship between number of disturbance rings and L/T and L/W ratios has been found in *Concinnithyris* sp. (order Terebratulida, family Terebratulidae Gray 1840) from the upper Cretaceous of Annopol on the Vistula, Poland (Fig. 11).

Normally, the growth of brachiopod shells follows a logarithmic spiral, i. e. shape remains the same during growth (see McGhee 1980). In the case of

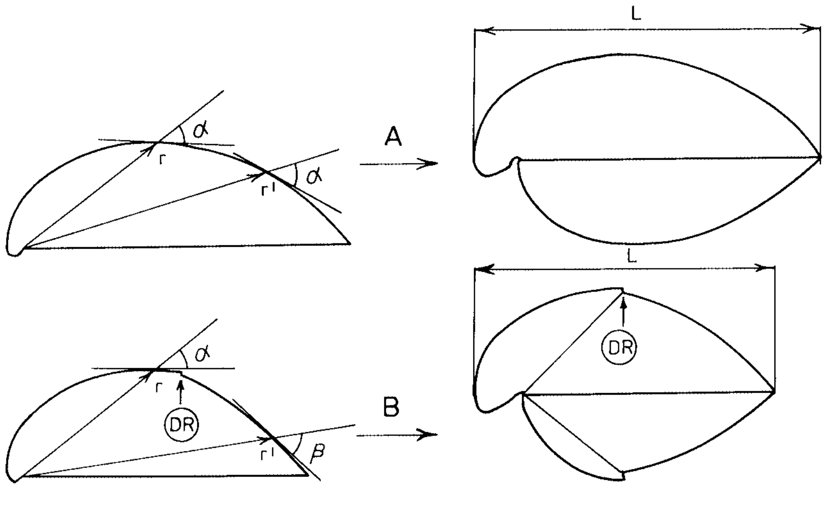

Fig. 12. Shell growth in specimens without disturbance rings (A) approaches an equiangular logarithmic spiral (with alpha remaining constant with increasing radius r). In specimens with disturbance rings (B) growth usually departese from the equiangular spiral with beta > alpha. This results in a change of shell shape. DR - disturbance rings, L - shell length.

C. vulgaris, only specimens without disturbance rings maintain a more or less equiangular logarithmic spiral growth throughout life (Fig. 12A), while specimens with disturbance rings deviate from the primary spiral: after each growth break the brachiopod continues to grow along a different spiral characterized by a slightly different angle between radius and spiral. The result is a change of the shell shape (Fig. 12B) and of the ratios L/T and L/W.

Shell curvature, which is characterized by the tangent angles to the spiral (alpha and beta; Fig. 12), depends on the relation between the rate of mantle growth and the rate of the shell growth. If both, mantle and shell, grow at the same rate, the shell becomes straight. The higher the growth rate of the shell is relative to mantle growth rate, the stronger is the shell curvature (and the higher the angle of the tangent to the spiral with the radius).

Because injuries resulting from environmental disturbance change the tangent's angle with the radius (Fig. 12), this disturbance also changed the relation between the growth rates of mantle and shell. After injury, either (1) mantle growth decreased (while shell growth remained the same), or (2) the rate of the shell secretion increased (and mantle growth remained constant), or (3) growth rate of the shell increased while mantle growth decreased at the same time.

In fossil material it is impossible to decide which of the three cases had been realized without a study of metabolism and shell growth in extant brachiopods, of the type carried out by ROSENBERG, HUGHES & TKACHUK (1988). Nevertheless it is interesting that the morphogenetic response to environmental disturbance may cause rather significant changes in shell morphology.

Evolutionary or ecological change?

As shown in Figures 2-4, there are marked differences in the frequency distribution of morphological characters (L/W and L/T ratios) between populations of *C. vulgaris* from the Upper and Lower Muschelkalk. Simultaneously, we have found (Figs. 9-10) that environmental disturbances producing rings modify the shape of the brachiopod shell by decreasing L/T ratio and increasing L/W ratio. This leads to the question whether the differences between populations of *C. vulgaris* from the Upper and Lower Muschelkalk have an evolutionary or an environmental origin.

It follows from both, MÜLLER's (1950) and our own data, that among 6 populations of *C. vulgaris* discussed in the present paper (Figs. 1 and 4), three lack forms with disturbance rings (Wolica, Marolterode, Jarugi), and three (Strzelce Opolskie, Reckenbühl, Döllstedter Trift) do comprise such forms. The mean L/T ratio in populations without disturbance rings (Fig. 4) is equal to 1.61 for population from the Lower Muschelkalk, in contrast to the Upper Muschelkalk, where the corresponding ratios are 1.98 (Jarugi), and 2.1 (Marolterode). If we consider only those specimens from Strzelce Opolskie (Lower Muschelkalk) that lack disturbance rings, the mean L/T ratio rises to about 1.8 (Fig. 10) - still less than for the Upper Muschelkalk populations. Thus, we see that Upper and Lower Muschelkalk populations of *C. vulgaris* show significant morphological differences which are independent from environmentally induced changes of shell shape. These differences in frequencey distribution of L/T and L/W ratios between *C. vulgaris* populations from the Lower and Upper Muschelkalk were caused either by evolutionary processes or by environmental factors which did not produce disturbance rings.

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