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Cathodoluminescence of Late Triassic terebratulid brachiopods: implications for growth patterns

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Abstract

Upper Triassic terebratulid brachiopod *Rhaetina* shows differential preservation of shell structure under cathodoluminescent (CL) and scanning electron microscope (SEM), indicating intra- and interspecific differences in brachiopod growth patterns.

In longitudinal sections, the CL lines appear firstly in inner, ontogenetically older parts of the shell and their outlines are parallel with the internal valve surface in posterior parts of the shell. In anterior parts of the shell, CL lines run diagonally towards the external valve surface and terminate in external growth lines. The shell structure of external growth lines indicates that major growth lines (associated with gradual reorientation of calcitic crystals due to reflection of the mantle edge) and disturbance lines (associated with abrupt mantle regression) are present at the terminations of CL lines. These data indicate that CL lines correspond to zones recording slowing/cessation of the growth rate. Under SEM, shell layers that are luminescent can be locally recognized as amalgamated or altered relicts of the secondary fibres. The origin of luminescence in these areas can be related to (1) the increased Mn-bearing diagenetic fluid flow favoured by higher porosity of altered secondary fibres, or can be caused by (2) temporal changes in the redox state controlling the solubility of Mn²⁺ and Fe²⁺ during the mantle anaerobiosis. Similarly, amalgamated/altered shell structure could either point to (1) the primary modification of shell secretory regime during the slowing/cessation in growth rate, or could be (2) the product of diagenetic processes responsible for post-depositional alteration of a shell structure, due to the primary shell heterogeneity/porosity in areas of growth discontinuities. Although presented data do not convincingly solve this uncertainty, the important point is that CL lines of studied brachiopods reflect changes in the growth rate and can be used in the investigation of growth dynamics in brachiopods, complementary to external growth lines and isotope or trace element analysis. In order to verify the modification of shell structure and understand the origin of associated luminescence during the change in growth rate unbiased by diagenetic overprint, it is necessary to examine modern brachiopods.

The distribution pattern of CL lines that correlates with growth rate fluctuations potentially reflects a short-term environmental instability on the time scale of an individual life span. The data show correlation between CL line pattern and different bathymetric settings. Regular repetition of CL lines is preserved in *Rhaetina gregaria*, *Rhaetina hybensis* and *Rhaetina pyriformis* that occur in relatively uniform depositional settings below a normal storm wave base. In contrast, irregular pattern of CL lines is typical of *R. gregaria* from highly variable deposit associations derived from very shallow, subtidal settings above

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a normal storm wave base. In the case of *R. gregaria*, this difference reflects intraspecific variations in growth dynamics among bathymetric settings, indicating environmental control on their growth rates. *Rhaetina gregaria* is mostly the only one brachiopod species present in benthic assemblages from very shallow, marginal marine environments in the Western Tethys. The implication is that *R. gregaria*, in contrast to most other brachiopods, could live in physically stressed habitats characterized by higher environmental instability/unpredictability.

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1. Introduction

The cathodoluminescence (CL) is the emission of photons in the visible range of the electromagnetic spectrum under cathodic excitation (Neuser et al., 1996). In calcium carbonate, the variation in CL intensity is generally attributed to the concentration ratio of activator (mainly Mn^{2+}) and inhibitor (mainly Fe^{2+}) ions (Machel, 1985; Machel et al., 1991; Savard et al., 1995). As concentrations of these elements in calcium carbonate are controlled by diagenetic processes (Veizer, 1983), they have been used to assess the evidence of diagenetic alteration in fossil invertebrates (Popp et al., 1986; Elorza and García-Garmilla, 1998; Voigt, 2000; Elorza et al., 2001; Rosales et al., 2001; Samtleben et al., 2001; Niebuhr and Joachimski, 2002; Voigt et al., 2003; see the review in Buening, 2001). However, Barbin and Gaspard (1995) showed that modern brachiopods can exhibit regular CL lines due to changes in the growth rate that correlate with temperature fluctuations, spawning seasons or environmental disturbance (see also Morrison and Brand, 1986; Barbin et al., 1991; Jiménez-Berrocoso et al., 2004). While this lowers the potential of the method for direct assessment of preservation of primary geochemical signals, CL lines can provide, in turn, information about growth patterns of brachiopods as related to their behaviour and ecology.

The main goal of this paper is to document shell preservation in the Upper Triassic terebratulids under CL and scanning electron microscope (SEM) and evaluate the relationships between CL lines, growth patterns and diagenesis. Although intra-shell trace element or isotope data are not available at this stage, a comparison of shell structure under SEM and CL provides interesting insights into the understanding of brachiopod growth patterns and diagenesis.

In most paleoecological analyses, data dealing with short-term (e.g., seasonal) variations in environmental factors are missing due to the effect of time-averaging of the fossil record (Walker and Bambach, 1971; Fürsich and Aberhan, 1990; Kowalewski, 1996; Olszewski, 1999). High-resolution isotope and trace element examinations of growth profiles of marine invertebrates provide an insight into short-term environmental variations and are widely used in paleotemperature and paleosalinity studies (Jones et al., 1983, 1989; Jones and Allmon, 1995; Krantz et al., 1987; Steuber, 1996, 1999; Goodwin et al., 2001, 2003; Ivany et al., 2003). Considering that the CL lines could reflect growth patterns as indicated by Barbin (1992) and Barbin and Gaspard (1995), then their distribution pattern should enable similar assessment of the brachiopod growth dynamics and the influence of environmental factors on the short-term time scale of years. The evaluation of growth rates is one of the most important tasks in the understanding of heterochrony, ecology and physiology of fossil and modern organisms (McKinney and McNamara, 1991; Jones and Gould, 1999; Dietl et al., 2002).

2. Paleogeography and stratigraphy

Samples are derived from the Upper Triassic carbonate deposits of the West Carpathians (Slovakia). Paleogeographically, the West Carpathians were situated on the extensive carbonate platform at the northwestern margin of the Tethys Ocean, in the subtropical climatic belt (Michalík, 1994; Fig. 1A). This carbonate platform was subdivided into several shore-parallel depositional settings, now preserved in various structural units (Haas et al., 1995; Gawlick et al., 1999). Terebratulid brachiopod *Rhaetina gregaria* was sampled in the Fatra Formation (Fatric Unit,

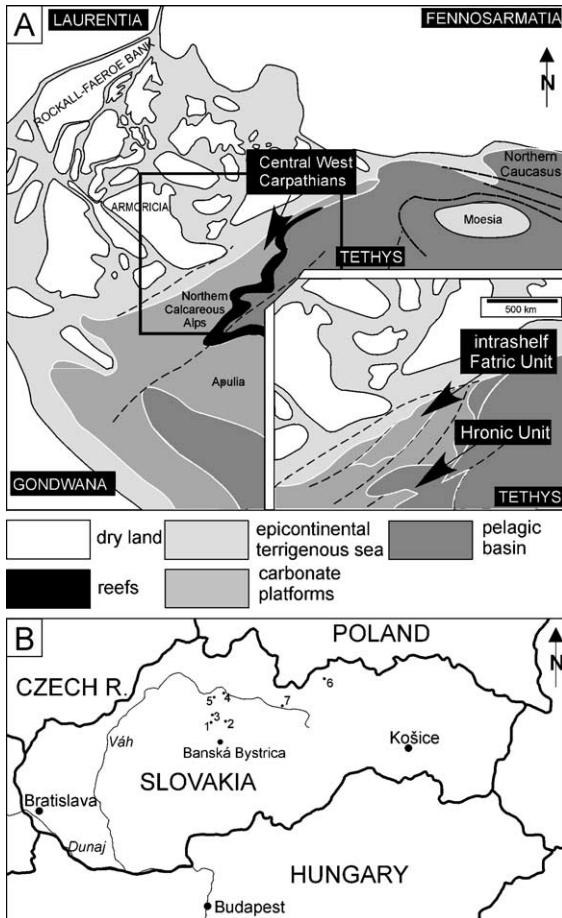


Fig. 1. (A) Paleogeographic position of the West Carpathians in the Upper Triassic (modified after Michalík, 1994). (B) Geographic location of the sampled sections in Slovakia. 1—Dedošova, 2—Sviniarka–Malý Zvolen, 3—Borišov, 4—Bystrý potok, 5—Ráztoky, 6—Kardolína, 7—Hybe. 1–6—Fatra Formation (Fatric Unit). 7—Hybe Formation (Hronic Unit).

Krížna Nappe) that represents predominantly carbonate deposition in a shallow intrashelf restricted lagoon, mostly above a normal storm wave base (Tomašových, 2004a). The Fatra Formation is formed by highly variable peritidal and shallow subtidal, carbonate facies associations, locally with claystone and dolomite intercalations and low terrigenous admixture (Michalík, 1982; Tomašových, 2004a). *Rhaetina hybensis* and *Rhaetina pyriformis* were sampled in the Hybe Formation (Hronic Unit, Choë Nappe) which originated in a more stable, open marine environment, mainly below a normal storm

wave base (Michalík, 1973, 1975). The Hybe Formation is composed of alternation of dark grey biomicritic limestones and marlstones, locally with tempestitic interbeds, and is comparable to the Eiberg Member of the Kössen Formation (Eastern Alps, Michalík, 1973; Golebiowski, 1991). Both formations are of Rhaetian age. *Rhaetina* is one of the most widely distributed brachiopod genera at the end of the Triassic. *Rhaetina gregaria* and *R. pyriformis* have a cosmopolitan distribution (Klören, 1974; Pearson, 1977; Sandy and Stanley, 1993; Siblík, 1998); *R. hybensis* is an endemic species known from the Hronic Unit only (Michalík, 1975).

3. Methods

The database includes 13 specimens of *Rhaetina gregaria*, one specimen of *Rhaetina hybensis* and one specimen of *Rhaetina pyriformis* (Table 1). *Rhaetina gregaria* was sampled at six localities of the Fatra Formation in the Veľká Fatra Mts. (Dedošova-DD, Sviniarka-Malý Zvolen-S, Bystrý potok-BP, Ráztoky-R, Borišov-B) and Belianske Tatry Mts. (Kardolína-K). Specimens DD5.2 (the bed number follows after the locality shortcut), S81.2-8, BP9.5.1-4, BP15.2-6, BP15.2-7a-c, R35-10, B9 and K35 are derived from bio-floatstones in close association with peritidal mudstones or biointra-packstones with signs of storm reworking (i.e., above the normal storm wave base). Specimens BP9.4.1-1, BP9.4.2-2 and BP9.4.2-3 are derived from bio-floatstones with minor physical postmortem disturbance (i.e., below the normal storm wave base). *Rhaetina pyriformis* and *R. hybensis* were sampled in floatstones/wackestones at the locality Hybe near Liptovský Hrádok (Fig. 1B, Table 1).

Preservation of shell structure under SEM was studied both in transversal and longitudinal thin-sections. Polished surfaces were etched with acetic acid (10%) for several seconds and coated with gold. The screening was done at the Comenius University and at the State Geological Institute of D. Štúr (Bratislava, Slovakia), using the JEOL-JXA 840A SEM. All exposures were taken at the black and white panchromatic negative film Fomapan 100 (21DIN / 100ASA).

The CL photomicrographs of brachiopod shells were performed using hot CL-microscope HC2-LM

Table 1
The database of specimens investigated under CL microscope

Specimen (ID)	CL micro-fractures (0—present, 1—absent)	CL lines (0—present, 1—absent)	Number of CL lines	CL line pattern	Species	Length of pedicle valve (mm)
<i>Internal structures</i>						
BP15.2-6	1	1	?	.	<i>R. gregaria</i>	10
BP15.2-7a	0	1	?	.	<i>R. gregaria</i>	14.2
B9	0	1	6	.	<i>R. gregaria</i>	21.2
BP9.4.2-3	1	1	8	.	<i>R. gregaria</i>	20.8
H21	1	1	9	.	<i>R. pyriformis</i>	50.5
<i>Posterior part</i>						
H20	1	1	9	regular	<i>R. hybensis</i>	33
DD5.2	1	1	8	regular	<i>R. gregaria</i>	16.1
9.4.2-3	1	1	8	regular	<i>R. gregaria</i>	20.8
B9	0	1	6	irregular	<i>R. gregaria</i>	21.2
R35-10	1	1	?	irregular	<i>R. gregaria</i>	20
BP15.2-7a	1	1	7	irregular	<i>R. gregaria</i>	14.2
BP15.2-7b	1	1	3	irregular	<i>R. gregaria</i>	16.8
BP15.2-7c	1	1	6	irregular	<i>R. gregaria</i>	13.8
BP15.2-6	1	1	4	?	<i>R. gregaria</i>	10
K35	1	1	?	?	<i>R. gregaria</i>	22
BP9.4.2-2	1	0	0	absent	<i>R. gregaria</i>	19.3
BP9.4.1-1	1	1	6	regular	<i>R. gregaria</i>	18
H21	1	0	0	regular	<i>R. pyriformis</i>	50.5
BP9.5.1-4	1	1	7	irregular	<i>R. gregaria</i>	10.1
S81.2-8	1	1	?	irregular	<i>R. gregaria</i>	14
<i>Anterior part</i>						
R35-10	1	1	2	.	<i>R. gregaria</i>	20
B9	0	1	5	.	<i>R. gregaria</i>	21.2
H21	0	1	?	.	<i>R. pyriformis</i>	50.5
K35	1	1	?	.	<i>R. gregaria</i>	22

The CL line pattern was evaluated only in the posterior part of shell. ID number starts with the letter referring to the locality. Explanations: DD—Dedošova, S—Sviniarka-Malý Zvolen, B—Borišov, BP—Bystrý potok, R—Ráztoky, K—Kardolína, H—Hybe.

(Simon-Neuser) at the Masaryk University, Brno, Czech Republic. The longitudinal thin-sections were coated with a carbon film and non-etched. As CL and SEM photographs were done under different magnifications, SEM mapping of shell parts which should correspond to CL lines required a detailed visual comparison. The recognition of CL lines under SEM was based on distance correspondence of CL lines and altered shell parts under SEM. If distances between CL lines (or between CL lines and the internal valve surface) under CL microscope and distances between altered shell parts (or between altered shell parts and the internal valve surface) under SEM were equal on the scale of 10 μm , CL lines and altered shell parts were considered to be identical.

Observations were carried out at 15-keV accelerating voltage, beam current of 0.2 mA and overall

magnifications from 4 \times to 10 \times . All observations were exposed at a colour reversal film Fujichrome multispeed MS100/1000, which has variable sensitivity from 100 to 1000 ISO. The film was exposed as 800 ISO and developed by conventional E-6 process. The film was pushed three times (push conditions=P-3) during the development procedure.

4. Results

The database of the specimens investigated under CL microscope is presented in Table 1. Localizations of shell parts photographed under CL are shown in Fig. 2 and CL and SEM photographs are illustrated in Figs. 3–7. In the following, the shape of fibres in transversal sections is described as it is used as a

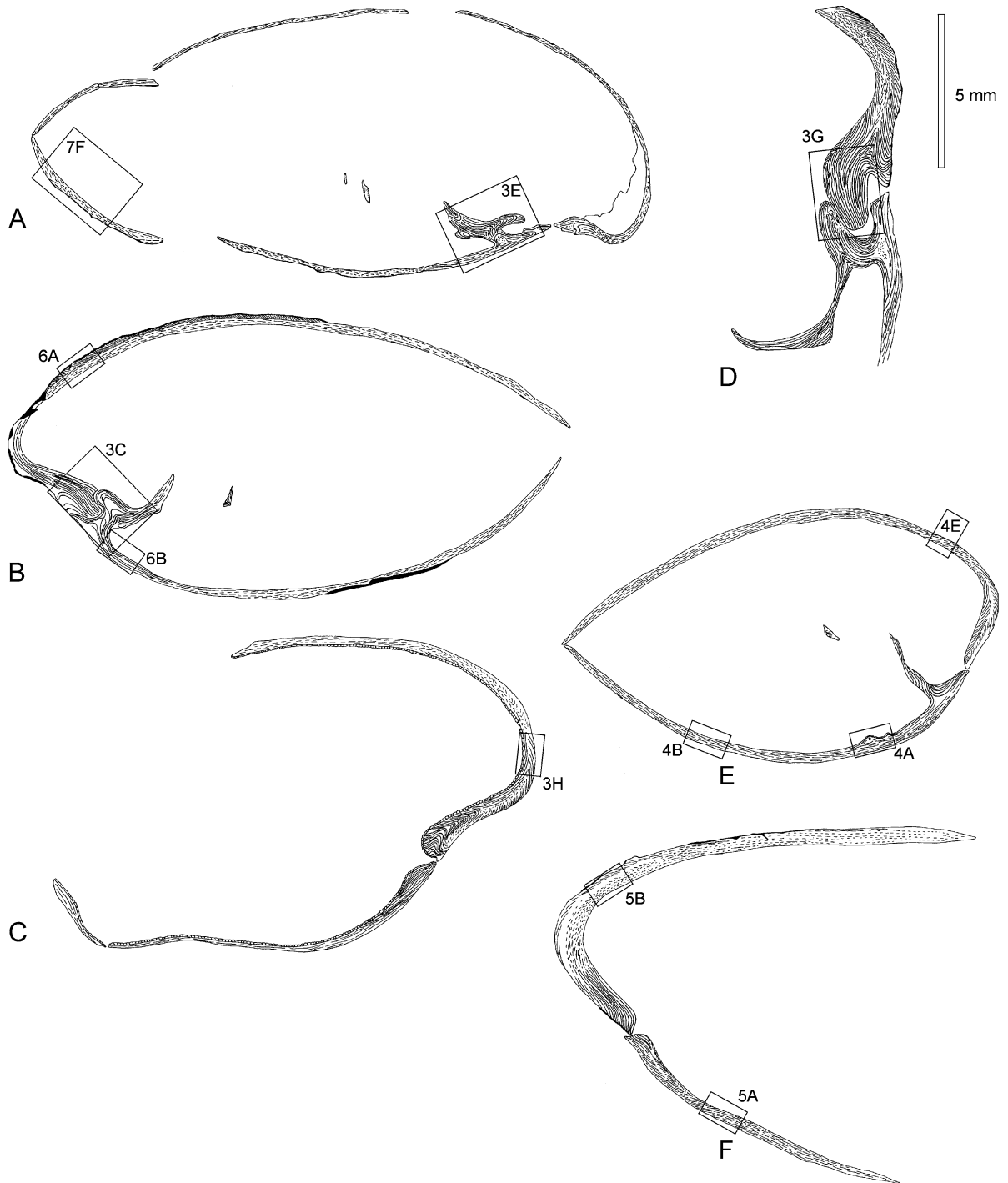
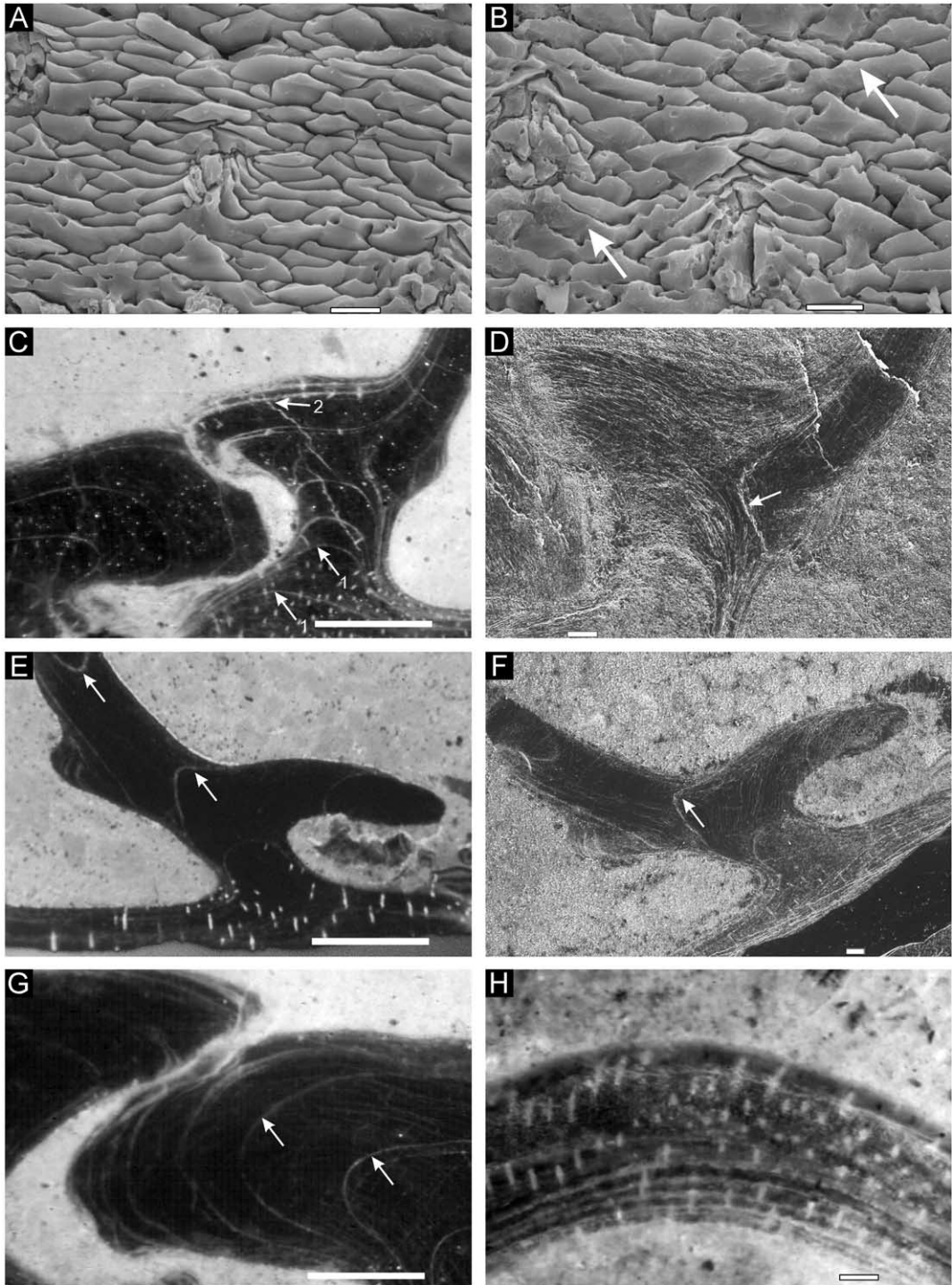


Fig. 2. Schematic drawings of longitudinal sections of brachiopod shells with localized areas that were photographed under CL. (A) *Rhaetina gregaria*, Borišov (B9), (B) *R. gregaria*, Bystrý potok (BP9.4.2-2), (C) *R. gregaria*, Dedošova (DD5.2), (D) *Rhaetina pyriformis*, Hybe-Kantorská (H21), (E) *R. gregaria*, Bystrý potok (BP15.2-7a), (F) *Rhaetina hybensis*, Hybe-Viper pit (H20).



conventional method in the evaluation of secondary layer preservation. Longitudinal sections were analyzed in order to see changes in shell structure in a growth direction. Internal structures (cardinalia and crural bases), and posterior and anterior parts of the shell are described in separate sections.

4.1. Transversal sections

The original anvil convex–concave shape of secondary fibres in transversal sections is well preserved in *Rhaetina hybensis* and *Rhaetina pyriformis* from the Hybe Formation (Fig. 3A) and in some specimens of *Rhaetina gregaria* from localities of the Fatra Formation (Bystrý potok). In some *R. gregaria* specimens from the Fatra Formation, secondary fibres are coalesced/amalgamated (Fig. 3B), their boundaries are irregular, angular or crenulated (see arrows in Fig. 3B), and blocky crystallites can also be present. In other specimens, rare simple microborings and regular, small-scale microgrowth increments of diurnal origin were observed. Intercrystalline organic matrix is absent.

4.2. Longitudinal sections

4.2.1. Internal structures

Internal structures (dental sockets, socket ridges and crural bases) of four specimens of *Rhaetina gregaria* and one specimen of *Rhaetina pyriformis* were observed under CL microscope (Table 1). A typical feature is the presence of thin, well-defined, orange CL lines with regular rhythmic pattern and outlines paralleling the outer shape of internal structures (Fig. 3C and G; see arrows). CL lines within the dental socket of the specimen B9 (Fig. 3E) probably correspond to the ontogenetically younger dental socket/cardinalia surfaces, later buried under the newly grown shell material. In the case of hinge

teeth and sockets, CL lines are almost concentric. Under SEM, some CL lines are visible as breaks or directional changes of secondary fibres (see arrows in Fig. 3D and F). In other specimens, rare irregular CL micro-fractures cutting regular CL lines are preserved (Fig. 3C; see arrow 2).

4.2.2. Posterior parts of shells

In all specimens the primary layer shows bright CL with similar intensity and coloration as a surrounding micritic matrix (Figs. 4E and 5B). The punctae are filled with sparitic, micritic or pyritic infillings. In the first two cases, the punctae infillings also show bright CL; in the third case, they are non-luminescent.

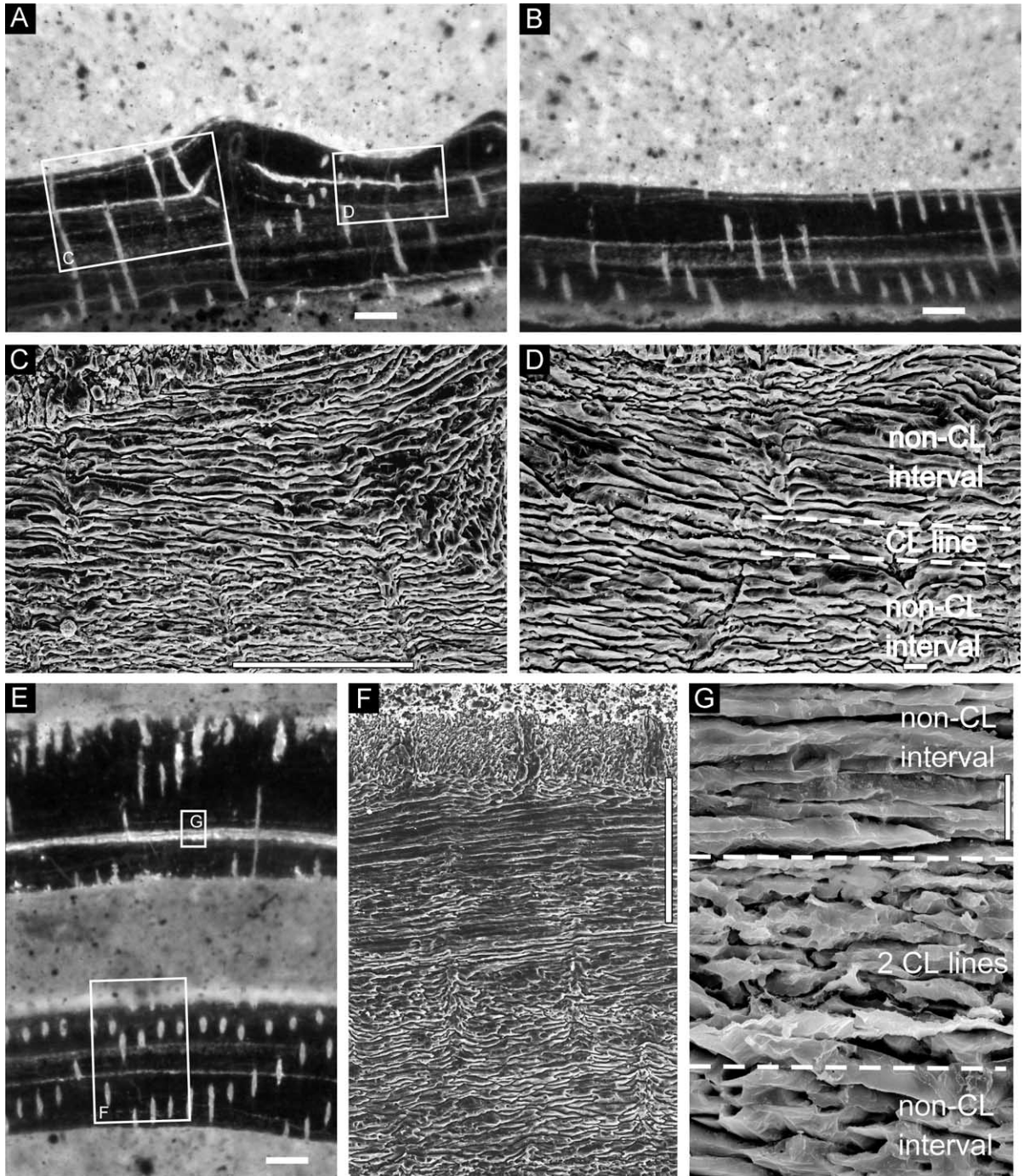
In *Rhaetina hybensis*, relatively thin and uniformly spaced CL lines are preserved in the posterior part of both dorsal and ventral valve. The CL lines are generally parallel with the internal valve surface and distances between lines are relatively constant (Fig. 5A and B). The high magnification (10×) revealed that some lines with intense luminescence are in fact consisting of two very closely spaced CL lines (Fig. 5A). In the dorsal valve (Fig. 5B), where whole valve thickness with primary layer is preserved, the first CL line appears in the middle part of the valve thickness. The upper, ontogenetically younger half of the valve thickness contains no CL lines. Under higher (50×) magnification, it can be observed that the number of CL lines is eight in the dorsal valve, and nine in the ventral one. Under SEM, the shell structure is formed by a relatively regular repetition of well preserved secondary fibrous layers (corresponding to non-luminescent lines) with typically amalgamated and irregular, 5–10-µm-thick, layers containing relicts of original secondary fibres (corresponding to CL lines) (Fig. 5C–F).

In *Rhaetina gregaria*, seven specimens show luminescence. The specimens derived from deposits with no signs of storm reworking (BP9.4.1-1,

Fig. 3. (A) Transversal section of unaltered secondary shell layer of *Rhaetina hybensis*, Specimen H20. Scale: 10 µm. (B) Transversal section of secondary shell layer of *Rhaetina gregaria*. Some fibres are amalgamated and their boundaries are locally angular or crenulated (see arrows), Specimen DD5.2. Scale: 10 µm. (C) Tooth and dental socket of *R. gregaria* under CL, with concentric CL lines (arrows 1) and irregular micro-fractures (arrow 2). Specimen BP9.4.2-2. Scale: 0.65 mm. (D) Tooth and dental socket of *R. gregaria* under SEM (same specimen as in Fig. 3C). Some CL lines correspond to a break or change in orientation of fibres (arrow). Specimen BP9.4.2-2. Scale: 100 µm. (E) Internal structure (dental socket and base of the loop) of *R. gregaria* under CL. The arrows point to CL lines. Specimen B9. Scale: 0.65 mm. (F) Internal structures (SEM) of *R. gregaria* (same specimen as in Fig. 3E). The arrow points to the zone corresponding to CL line, Specimen B9. Scale: 100 µm. (G) Hinge tooth and dental socket of *Rhaetina pyriformis*, with concentric CL lines (see arrows), Specimen H21. Scale: 0.65 mm. (H) The posterior part of a ventral valve of *R. gregaria*, with relatively regular pattern of CL lines. Specimen DD5.2. Scale: 100 µm.

BP9.4.2-2 and BP9.4.2-3) exhibit relatively regularly spaced CL lines, commonly parallel with the internal valve surface (Fig. 6A and B). In contrast, the CL

lines of other specimens (i.e., those derived from deposits originating above the normal storm wave base) have irregular spacing and thickness (Fig. 4A).



The only exception is the specimen from Dedošova (DD5.2), showing relatively regular spacing of CL lines. Note that the same pattern of irregularly thick CL lines can be preserved in both valves of some specimens (Fig. 4B and the lower valve in Fig. 4E; specimen BP15.2-7a).

The parallel CL lines in posterior part gradually pass into concentric CL lines preserved within internal structures (cardinalia). In three well-preserved specimens (BP9.4.2-2, BP15.2-6, DD5.2), the outer, ontogenetically younger part of the valve thickness contains no CL lines, similarly as in *Rhaetina hybensis*. The number of CL lines in posterior parts of shells mostly reaches six to eight. In specimen BP15.2-7b, two relatively thick and closely spaced CL lines are present in the middle part of the valve thickness (Fig. 4E). In most specimens, irregular micro-fractures are present locally, parallel or perpendicular to the internal valve surface. Under SEM, repetition of layers with different shell structure is not as obvious as for *R. hybensis*. In some cases, there are subtle changes in the amalgamation of secondary fibres which may correspond to CL lines (Figs. 4C,D and 6C,D). In other cases, no visible change in the shell structure is observable (Figs. 4F,G and 6E).

4.2.3. Anterior parts of shells

The anterior part of shell was observed in 4 specimens. In contrast to more posterior parts of valves, CL lines run obliquely from the internal valve surface towards external surface (Fig. 7F). Here, they often terminate in subtle external elevation or break, corresponding to external growth line. Towards the anterior margin, CL lines are becoming more closely spaced. Under SEM, shell structure is well differentiated into layers with non-amalgamated and relatively well preserved secondary fibres (corresponding to non-luminescent zones) and 10–20- μ m-thick bands (corresponding to CL lines) that exhibit

amalgamated and irregular or relict secondary fibres (Fig. 7A–E). The latter type runs obliquely towards the external surface and terminates in subtle external elevation/break (external growth line). This is associated with shift or dislocation of the primary layer. In some cases, reorientation of secondary fibres and primary layer is gradual (reflections sensu Williams, 1971; Fig. 7D); in other cases there is a visible dislocation between primary and secondary shell material (mantle regressions sensu Williams (1971), Fig. 7A and B).

5. Discussion

5.1. Growth-related luminescent lines

CL lines in modern brachiopods and other marine invertebrates were correlated with periods of slow growth rates, such as winter, spawning seasons or environmental disturbance (Barbin, 1992; Barbin et al., 1991; Barbin and Gaspard, 1995). However, in the case of brachiopods this was clearly shown in modern taxa only. There is relationship between the trace-element content of invertebrate skeletons and environmental conditions (Harris, 1965; Rosenberg, 1980). It is usually supposed that (1) either the proportion of the Mn is constant in external environment and it is only a differential growth rate that affects variation in the Mn content of carbonate skeletons, or (2) the Mn content of external environment is variable, causing differences in the Mn content of carbonate skeletons (Barbin et al., 1991).

The evidence that CL lines preserved in *Rhaetina* shells correspond to zones of primary growth origin consists of (a) regular and non-random pattern of CL lines in some specimens, in coherence with outlines of growth surfaces (e.g., hinge teeth or crura); (b) CL lines in anterior parts terminate in external growth

Fig. 4. (A) The posterior part of a dorsal valve of *Rhaetina gregaria* with irregular pattern of CL line, Specimen BP15.2-7a. Scale: 100 μ m. (B) The posterior part of a dorsal valve of *R. gregaria*, Specimen BP15.2-7a (the same specimen as lower ventral valve in Fig. 4E). Note that the irregular pattern of CL lines is similar to that in the ventral valve. Scale: 100 μ m. (C) The posterior part of a dorsal valve of *R. gregaria* (corresponding to Fig. 4A). Specimen BP15.2-7a. Scale: 100 μ m. (D) Detail of (C). Slight changes in the shell structure correspond to CL line (delimited by white lines). Scale: 10 μ m. (E) Posterior parts of two ventral valves of *R. gregaria* with the irregular pattern of CL lines. Specimens BP 15.2-7b (the upper valve) and 7a (the lower valve). Scale: 100 μ m. (F) The posterior part of a ventral valve of *R. gregaria* (corresponding to the lower valve on Fig. 4E). The pattern of CL lines is not apparent under SEM, Specimen BP 15.2-7a. Scale: 100 μ m. (G) The posterior part of a ventral valve of *R. gregaria* (corresponding to the upper valve on Fig. 4E). Altered shell structure corresponds to two thick, almost fused CL lines, Specimen BP15.2-7b. Scale: 10 μ m.

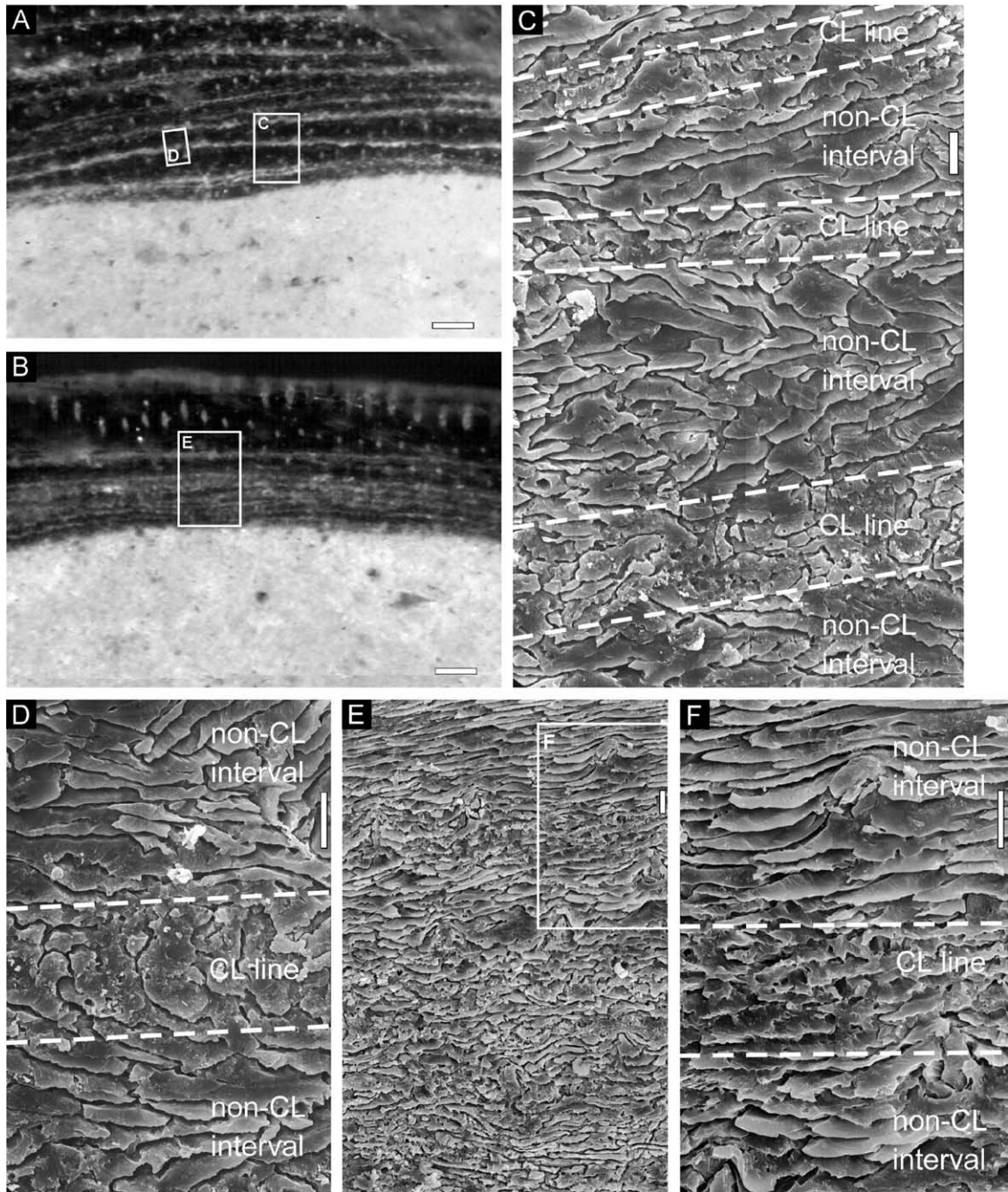


Fig. 5. *Rhaetina hybensis*, Specimen H20. (A) The posterior part of a dorsal valve with regular pattern of CL lines. Scale: 100 μm . (B) The posterior part of a ventral valve with regular pattern of CL lines. Scale: 100 μm . (C) Longitudinal section in the posterior part of a ventral valve (detail of Fig. 5A). The repetition of layers with different shell structure is visible. Layers with amalgamated/altered structure correspond to CL lines. Scale: 10 μm . (D) Detail of Fig. 5C. Scale: 10 μm . (E) The repetition of unaltered (non-CL intervals) and altered (CL lines) shell structure in the dorsal valve (detail of Fig. 5A). Scale: 10 μm . (F) Detail of (E). Amalgamated/altered shell layer corresponds to the first, ontogenetically youngest CL line. Scale: 10 μm .

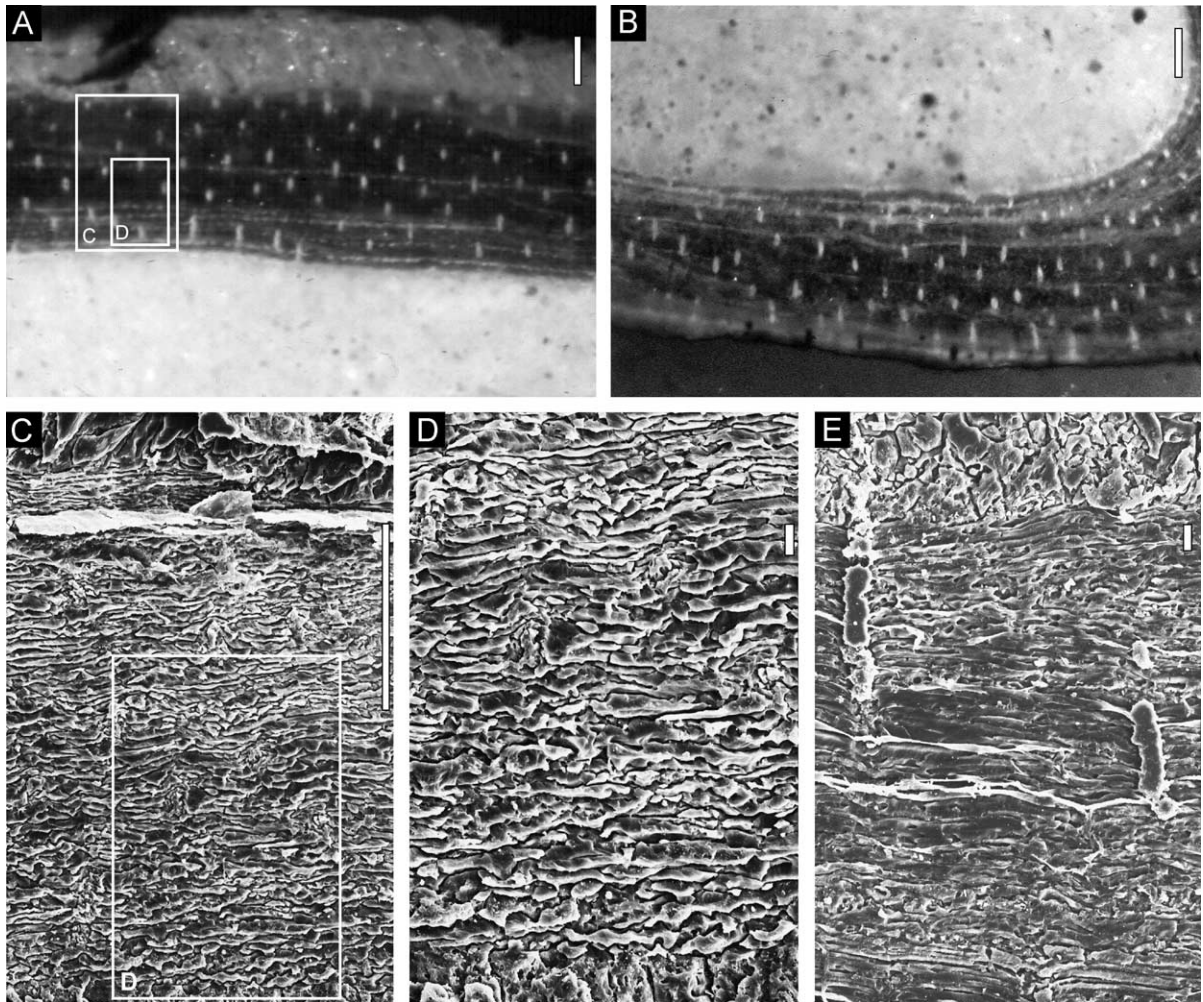


Fig. 6. (A) The posterior part of a dorsal valve of *Rhaetina gregaria* with regular pattern of CL lines. Specimen BP 9.4.2-2. Scale: 100 μ m. (B) The posterior part of a dorsal valve of *R. gregaria*, Specimen BP 9.4.2-2. Scale: 100 μ m. (C) Shell structure of the posterior part of a ventral valve of *R. gregaria* (corresponding to Fig. 4A under CL), Specimen BP 9.4.2-2. Scale: 100 μ m. (D) Detail of (C). Note that repetition of bands with different shell structure is obscured. Scale: 10 μ m. (E) The posterior part of a dorsal valve; CL lines are not detectable in the shell structure. Specimen B9. Scale: 10 μ m.

lines; and (c) the first CL lines appear in inner (i.e. ontogenetically older) parts of valves.

Regular repetition of CL lines of uniform width and spacing, with outlines approaching the shape of internal structures, indicates that the formation of corresponding zones was related to the growth dynamics of brachiopod shell. In some shells of *Rhaetina gregaria*, the width and spacing of CL lines are more irregular, but their direction and outline remain parallel or convergent with the outlines of internal morphological characters. This is particularly

visible in specimen BP15.2-7a, where the same conspicuous pattern of CL lines is preserved in both dorsal and ventral valve (Fig. 4B and the lower valve in Fig. 4E). In contrast, irregular CL micro-fractures are mostly cross-cutting morphological characters, and usually exhibit brighter luminescence that indicates their diagenetic origin.

Termination of CL lines in external growth lines in anterior parts of shells is another important evidence that they trace original growth surfaces. Their curvature towards the external surface is in accord

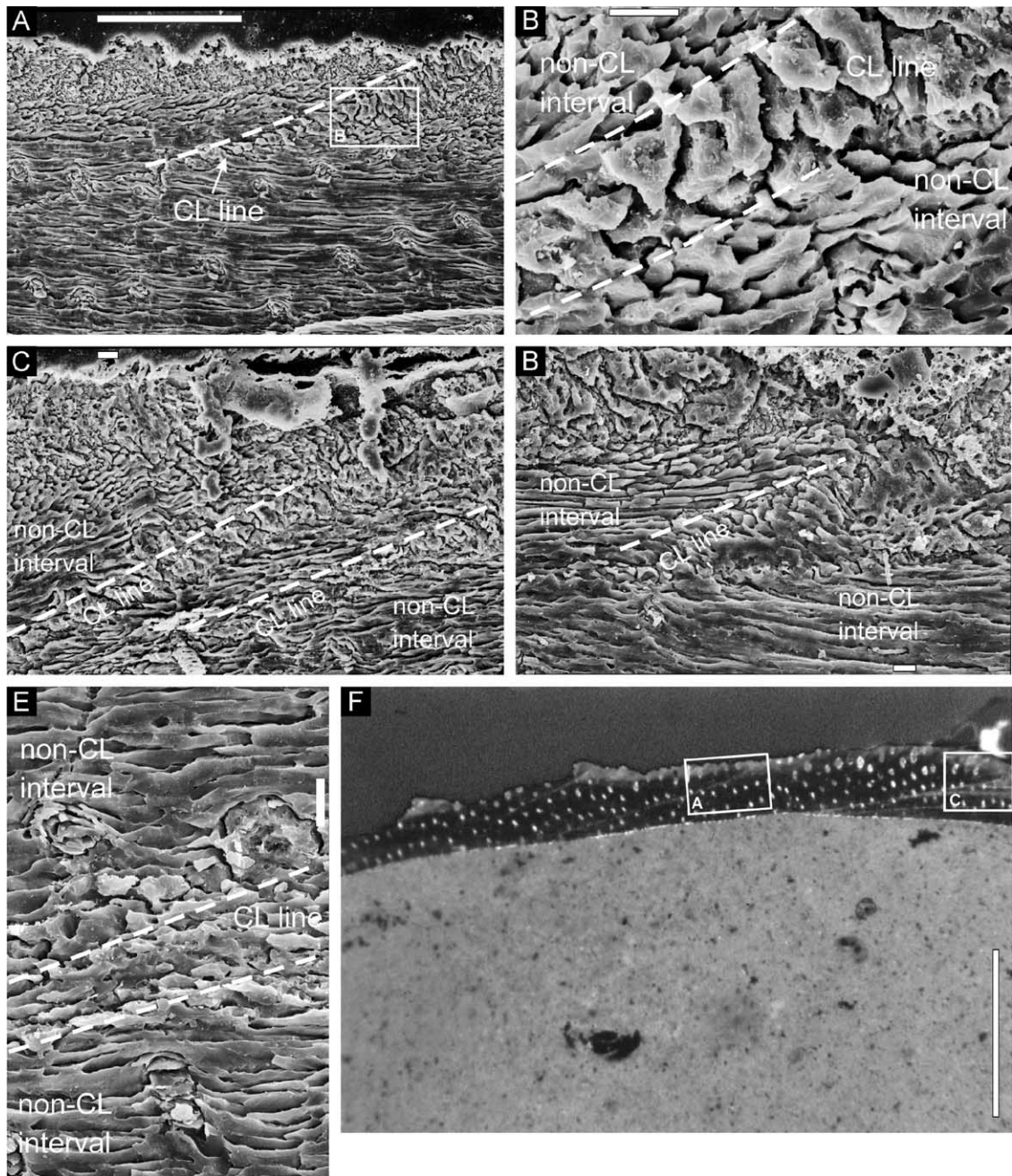


Fig. 7. *Rhaetina gregaria*, the anterior part of a dorsal valve, Sample B9. (A) The structure of CL line (see arrow) is formed by amalgamated structure of secondary shell layer in the anterior part of a dorsal valve. There is an abrupt shift in the primary layer, corresponding to mantle regression. Scale: 100 μm . (B) Detail of (A). Scale: 10 μm . (C) Two interlayers with amalgamated/altered shell structure, corresponding to CL lines in the anterior part of a dorsal valve. Scale: 10 μm . (D) External growth line in the anterior part of a dorsal valve, corresponding to the termination of CL line. Gradual reorientation of fibres is visible, corresponding to a gradual mantle reflection. Scale: 10 μm . (E) Detail of amalgamated/altered shell structure, corresponding to CL line, in the anterior part of a dorsal valve. Scale: 10 μm . (F) The anterior part of a dorsal valve under CL microscope, with visible CL lines converging towards the external surface. Scale: 0.65 mm.

with the growth of brachiopod valve on its margin. The spatial coincidence of CL lines with external growth lines is the direct evidence that the growth rate was slowed or stopped in the zone now corresponding to a CL line.

Juvenile brachiopods grow relatively rapidly during the first several months of their life (although there is a short lag phase for juveniles 0.5 mm long, cf. Doherty, 1979; Collins, 1991). The growth rate then gradually decreases from about the third year of their life (Thayer, 1977; Curry, 1982), leading eventually to growth cessation in adults (Doherty (1979) observed no growth of 14 tagged adults over a period of 248 days). The consistent appearance of CL lines in inner (ontogenetically older) parts of valves and their absence in outer (ontogenetically younger) parts can be interpreted in terms of rapid growth rate during the earlier life stages of brachiopod lives (Barbin and Gaspard, 1995).

5.2. Diagenetic influence versus primary biologic control of shell structure

The degree of the secondary layer alteration is supposed to reflect the intensity of diagenetic processes (see above). Samtleben et al. (2001) showed that relatively regular CL lines in Silurian atrypid brachiopods corresponding to coarsely crystalline, amalgamated layers alternate with unaltered secondary layers. This is typically interpreted as a product of diagenetic alteration. However, it is known that some phenomena that are related to primary biologic processes can lead to altered/degraded state of preservation of the secondary layer. These include (a) incomplete shell secretion and (b) resorption of previously deposited shell material (such as during mantle anaerobiosis, or due to muscle activity or differential growth of internal structures, see Williams, 1971; Hughes et al., 1998; Gaspard, 1986, 1993, 1996).

As the change in the shell structure could be the product of biologic growth patterns, altered shell structure and associated CL lines (cf. Barbin and Gaspard, 1995) are not direct evidence that brachiopod shell was substantially affected by diagenetic processes. For isotope measurements, just to be on the safe side, it can be argued that even if altered shell structure and associated CL lines are of primary origin,

they still represent zones of discontinuity that can be preferentially affected during the diagenesis (i.e., they can be diagenetically enhanced growth lines). Under SEM, altered shell parts show higher porosity that can enhance increased flow of diagenetic fluids (Henrich and Wefer, 1986). In belemnites, such primary growth pattern is overprinted by diagenetic alteration due to intercrystalline degradation of organic matter (Saelen, 1989; Podlaha et al., 1998; Elorza et al., 2001). This secondary overprint of CL lines is locally visible also in the studied terebratulid shells, where CL lines that form a regular pattern are fused with irregular microfractures, characterized by higher intensity of luminescence (e.g., Fig. 3C; see arrow 2).

5.3. Shell structure of CL lines

Interpretation of CL lines as a primary biologic or secondary diagenetically enhanced record of changes in the growth rate has an important role for understanding of growth patterns in fossil brachiopods. Unfortunately, processes responsible for the formation of internal growth increments and growth lines are still relatively poorly understood for brachiopods (Hiller, 1988; Hughes et al., 1998; Rosenberg et al., 1988). As the shell structure of CL lines corresponds to amalgamated and irregular calcitic layer with relicts of original secondary fibres in both posterior and anterior parts of some specimens, it can be that change in the growth rate was associated with change in shell secretory regime. In modern brachiopods a deposition of calcite pads and/or high proportion of organic matrix, controlled by retracting mantle lobe, has been documented on the exposed faces of calcite fibres (Williams, 1971). If the amalgamation/alteration of secondary fibres is primarily a consequence of the decrease or cessation in the growth rate, two alternative hypotheses can explain the change in the shell structure:

- (1) During the retraction of outer mantle lobe from its normal position, the normal secretory regime of the outer epithelium is interrupted, the external growth line is formed and a temporarily different type of shell secretion can take place. When mantle retraction has ended, the retracted part of mantle undergoes microscopic readjustments as each cell responsible for the secretion

of calcite starts secreting a calcifying pad in continuity with the terminal face of another fiber (Williams, 1971; Hiller, 1988). In addition, outer epithelial cells can secrete a relatively high proportion of organic matter either before or during retreat (Williams, 1971).

- (2) During growth cessation due to environmental stress (e.g., tidal exposure or storm disturbance) shells can be closed for a relatively long time (i.e., on the scale of several hours/days). The organic acid by-products of mantle anaerobiosis are buffered by dissolution of the previously deposited secondary shell layer (Lutz and Rhoads, 1977). Short intervals of lower pH levels in the mantle cavity of modern *Terebratalia transversa*, in response to tidal cycles, led to the dissolution of portions of the inner shell layers (Hughes et al., 1998). Elorza et al. (2001) documented that CL lines in Cretaceous inoceramid bivalves correspond to organic-rich areas that can be related to a decalcification process that leads to an increase in the proportion of acid-insoluble organic material. Moreover, the changes in pH affect also the redox state and solubility of Mn^{2+} and Fe^{2+} , the key ions driving the CL intensity in calcium carbonate.

In order to test these hypotheses, it is necessary to look in detail at the shell structure of CL lines of modern brachiopods under SEM. In this case, the possible preferential attack of growth discontinuities by diagenetic fluids can be excluded and alteration of shell structure will be a consequence of pre-mortem biologic processes only. This is supported by an observation of Barbin and Gaspard (1995). They reported that CL lines in modern brachiopods correspond to zones enriched in organic matter, indicating reduced calcitic secretion and comparatively higher secretion of organic matter by the protein secretory zone of a cell.

5.4. Implications for growth patterns and ecology

It is possible that activation of CL due to higher Mn/Fe ratio and amalgamation of secondary fibres under SEM represent diagenetic overprint at the zones of inhomogeneity/discontinuity. However, spatial arrangement of CL lines and their association with

external growth lines indicate that they correspond to the zones reflecting the period of relatively slow growth rate or its cessation. CL lines can thus provide a complementary line of evidence about growth dynamics, which can be used together with external growth lines, internal growth increments, and stable isotope or trace element signals along the shell profile.

According to Hiller (1988), the examination of longitudinal sections of shells allows for the detection of short-term disturbance lines from major seasonal or periodic growth lines. Following this criterion, the shell structure of *Rhaetina* growth lines indicates that major growth lines (associated with gradual reorientation of primary and secondary layer due to reflection of the mantle edge) and disturbance lines (associated with abrupt mantle regression) are present at the terminations of CL lines. The question of timing and duration of growth rate cessation represented by CL lines is very important for a direct estimate of absolute growth rate and age of brachiopods. A relatively constant number of CL lines in the posterior parts of adult shells of *Rhaetina gregaria* (6–8) and *Rhaetina hybensis* (8–9) hints at regular seasonal/annual changes in the growth rate, perhaps indicating an age that spans the period of several years.

As the growth pattern may potentially reflect short-term environmental instability/predictability on the scale of individual life span, it is possible to test if there is a correlation between CL line growth pattern and distribution of *Rhaetina* in particular environmental settings.

Regular pattern of CL lines is exhibited by *Rhaetina hybensis* and *Rhaetina pyriformis*. These two species occur in bioturbated marlstones and biomicritic limestones of the Hybe Formation, locally with tempestitic coquinal interbeds, indicating an environment below or around the maximum storm wave base (Michalík, 1973). The benthic association is relatively diverse and consists of other brachiopods, bivalves, gastropods, bryozoans, serpulids and nautiloids. Similarly, regular rhythmic repetition of CL lines in *Rhaetina gregaria* is typical of floatstone deposits (Bystrý potok section, beds 9.4.1–9.4.2) originating near the maximum storm wave base (for taphonomic analysis of brachiopod beds see Tomašových, 2004b). In contrast, an irregular pattern of CL lines (variation in width of CL lines, gradational or abrupt boundaries) is typical of *R. gregaria* specimens

from tempestitic deposits originating above the normal storm wave base, or closely associated with peritidal facies. Here, they are present in poorly diverse, almost monospecific associations. In this case, general differences in the depth/storm wave base can be potentially correlated with short-term environmental variations/instability (e.g. frequency of storm disturbance). This preliminary correlation indicates that stable and relatively predictable ecological conditions were typical of the habitat of *R. pyriformis* and *R. hybensis* from the Hybe Formation, and less common for *R. gregaria* from the Fatra Formation.

In the fossil record, the relationship between short-term environmental variations and life history traits was documented by Sato (1999) in Pleistocene bivalves or by Good (2004) in Late Jurassic freshwater bivalves. In modern brachiopods, intraspecific variations in growth rates can be relatively high (Paine, 1969; Thayer, 1977; Rickwood, 1977; Doherty, 1979). The correlation between water depth and brachiopod growth rates/mean shell size was shown by McCammon (1973), Rickwood (1977), Aldridge (1981), Stewart (1981) and Witman and Cooper (1983). Typically, a decrease in growth rates or stunting is interpreted to take place in suboptimal environments. The differential intraspecific growth patterns among different environments were described in several fossil brachiopods. Based on growth line-frequency analysis, Curry (1984a,b) proved that two populations of the Tertiary brachiopod *Bouchardia antarctica* show the same life span but different growth rates. Trammer et al. (1996) showed a relationship between number of disturbance rings (controlled by storm frequency) and shell shape in the Triassic brachiopod *Coenothyris vulgaris*, clearly indicating environmental control on growth patterns. Based on different number of prominent growth lines, Johnson (1989) revealed intraspecific differences in the life span of Silurian *Pentamerus oblongus* between shallow and deep environments. He attributed this to different frequencies of storm disturbance along a depth-related gradient. With similar reasoning, *Rhaetina gregaria* shows differential growth pattern between shallow and deep habitats. In the habitats above the normal storm wave base, the changes in the growth rate were more irregular/unpredictable in comparison to the deeper habitats below the normal storm wave base.

In the Carpathians and Alps, *R. gregaria* generally rarely co-occurs with other brachiopod species (Michalík and Jendrejáková, 1978; Golebiowski, 1991). In contrast, *Rhaetina pyriformis* and *Rhaetina hybensis* are typically present in benthic assemblages with other articulate brachiopods. This indicates that the distribution of *R. gregaria* in the shallowest deposits could be linked to its ability to live in habitats affected by short-term environmental instability/unpredictability, in contrast to other brachiopods. Indeed, in samples where *R. gregaria* is characterized by a uniform CL line pattern (Bystrý potok section, beds 9.4.1–9.4.2), other brachiopods are present, indicating more stable conditions. It is usually supposed that Mesozoic brachiopods were uncommon in physically stressed habitats (Aberhan, 1994). *Rhaetina gregaria* can be an exception to this general statement.

6. Conclusions

(1) Upper Triassic terebratulids show differential preservation of shell structure under CL microscope, most probably reflecting differences in growth rate pattern. In *Rhaetina hybensis*, *Rhaetina pyriformis* and *Rhaetina gregaria*, consistent rhythmic pattern of CL lines with uniform width and spacing is typical. In some specimens of *R. gregaria*, this pattern of CL lines can be much more irregular, formed by CL lines of variable width and spacing.

(2) The CL lines appear firstly in inner, ontogenetically older parts of the shell. In posterior shell parts their outlines are parallel to the internal valve surface. In anterior parts of shells the CL lines run obliquely towards the external surface and terminate in external growth lines. This repetition of luminescent and non-luminescent lines within the secondary layer is here interpreted as a primary or diagenetically enhanced reflection of changes in growth rate. The origin of luminescence in the CL lines can be related to (1) the increased diagenetic fluid flow favoured by higher porosity of altered secondary fibres or can be due to (2) a primary change in the redox state and solubility of Mn^{2+} and Fe^{2+} during the periods of mantle anaerobiosis.

Under SEM, shell layers that are luminescent can be locally recognized as amalgamated or altered

relicts of the secondary fibres. If this alteration of the shell structure corresponds to the primary change in shell secretion, it could be caused by (1) the retraction of outer mantle lobe and its readjustment, with concomitant calcitic pad/organic-rich layer production, or (2) dissolution of previously deposited secondary layer due to a drop in pH in the mantle cavity during the mantle anaerobiosis.

(3) The distribution pattern of CL lines in *Rhaetina* shells varies between distinct bathymetric settings. Shells of *Rhaetina gregaria*, *Rhaetina hybensis* and *Rhaetina pyriformis* from an environment below the normal storm wave base show regular and rhythmic repetition pattern of CL lines of uniform width and with abrupt boundaries between CL lines. In *R. gregaria* from more shallow settings originating above the normal storm wave base, the CL line pattern is much more irregular, boundaries are gradational or abrupt and width of CL lines is very variable. This second pattern is probably the consequence of higher environmental instability in more shallow settings on the short-term time scale. In the case of *R. gregaria*, the difference in the CL line pattern probably reflects intraspecific variations in growth dynamics among bathymetric settings, indicating environmental control on the growth rates. Such differential growth patterns provide useful insights into brachiopod ecology. In the Western Tethys, *Rhaetina gregaria* typically occurs in monospecific or paucispecific assemblages in the shallowest habitats (Sandy, 1995), with other brachiopods species being very rare or absent (Golebiowski, 1991). This points to the possibility that this species was physiologically adapted to live in habitats characterized by higher environmental instability/unpredictability, mostly inaccessible to other articulate brachiopods.

(4) The analysis of CL lines can provide another important tool for evaluation of brachiopod growth rates, in addition to external growth lines (Curry, 1982, 1984a,b), zonal isotope (Buening and Spero, 1996; Jones and Quitmayer, 1996; Samtleben et al., 2001; Auclair et al., 2003; Goodwin et al., 2001, 2003; Ivany et al., 2003) and/or trace element data (Buening and Carlson, 1992; Steuber, 1996, 1999). Systematic examination of CL line patterns can lead to better understanding of brachiopod biology and add detail to paleoenvironmental analysis.

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