## BORING FORAMINIFERA FROM EXOTICS OF THE ŠTRAMBERK-TYPE LIMESTONES (TITHONIAN–LOWER BERRIASIAN, POLISH CARPATHIANS)

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**Abstract:** The boring foraminifera *Troglotella incrustans* has been recorded in exotic boulders of the Štramberk-type limestone (Tithonian–lower Berriasian) occuring in the Polish Flysch Carpathians. In the studied material *Troglotella* occurs in association with *Lithocodium aggregatum*. The foraminiferal nature of this microproblematicum is accepted herein. The co-occurrence of both foraminifers is interpreted as a life association. *Troglotella* facultatively lived inside chambers of *Lithocodium* or bored in the carbonate skeletal substrate encrusted by it. On 5 mm of substrate as many as 10–15 borings–produced by *Troglotella* have been found. This poorly known foraminifera was described up to now from the Upper Jurassic. New data from other regions suggest that the stratigraphical range of the *Lithocodium-Troglotella* association should be extended to the Albian.

Abstrakt: W wapieniach egzotykowych typu sztramberskiego (tyton-dolny berias) występujących w polskich Karpatach fliszowych stwierdzono obecność drążących otwornic *Troglotella incrustans*. W badanym materiale, otwornice te występują w asocjacji z *Lithocodium aggregatum*. Według autora takson ten należy zaklasyfikować do Foraminiferida. Współwystępowanie obu otwornic miało miejsce za ich życia. *Troglotella* żyła w komorach *Lithocodium* lub drążyła w elementach szkieletowych inkrustowanych przez tą otwornicę. Na odcinku 5 mm powierzchni inkrustowanej przez *Lithocodium* można miejscami stwierdzić 10–15 wydrążeń wykonanych przez *Troglotella*. Ta słabo znana otwornica opisywana była dotychczas z górnej jury. Na podstawie nowych danych pochodzących z innych obszarów należy rozszerzyć zasięg stratygraficzny asocjacji *Lithocodium-Troglotella* do albu.

Key words: Foraminifera, symbiosis, bioerosion, Tithonian-Berriasian, Polish Carpathians.

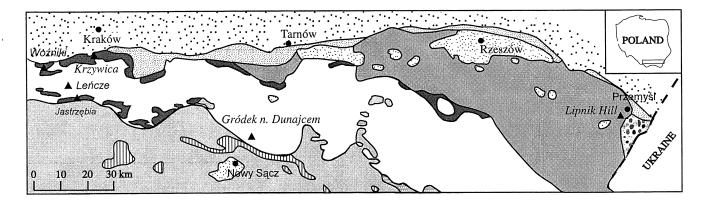
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#### INTRODUCTION

Foraminifera have adopted a variety of lifestyles, but not numerous among them have boring potential. Some foraminifers bore mainly to provide anchorage for the test, other ones are able to create crypts for themselves. About 20 species of fossil and modern boring foraminifera are known (for review see Plewes *et al.*, 1993; Vénec-Peyré, 1996). The oldest boring foraminifers are known from the Callovian (Plewes *et al.*, 1993). Mesozoic examples are much more rare then Cenozoic and Recent ones.

Abundant borings produced by foraminifers have been recorded in the Štramberk-type limestones. These limestones occur as exotic pebbles and boulders within the uppermost Jurassic, Cretaceous and Tertiary flysch sequences of the Polish Outer Carpathians. The Štramberk-type limestones is the age and facies equivalent of the Štramberk Limestone from Moravia (e.g., Eliáš & Eliášová, 1984). Štramberk facies is traditionally regarded as Tithonian age,

however, lower Berriasian calpionellids have been recorded both in Poland (Geroch & Morycowa, 1966; Morycowa, 1968) and Moravia (Houša, 1990). A lower Beriassian ammonitic fauna in the Štramberk Limestone has been recorded lately by Eliáš and Vašiček (1995). Its oldest part probably represents also the upper part of the lower Tithonian (Houša, 1990). In the strict sense the term Štramberktype limestones should be applied to reef deposits. According to Hoffmann (1992), these limestones represent coralthrombolite boundstone, which built patch reefs within cortoidal and grapestone facies in the calm environment of temporary agitated lagoons. Scleractinian corals are a main member of the constructor guild. The dense to peloidal microbial crusts and accompanying micro-encrusters are abundant in the limestones. Common micro-encrusters are Lithocodium aggregatum, Bacinella irregularis, "Tubiphytes" morronensis and Koskinobullina socialis.





**Fig. 1.** Geologic sketch-map of part of the Polish Outer Carpathians (after Książkiewicz, 1972; partly changed): I – Magura Unit; 2 – Grybów Unit; 3 – Dukla Unit; 4 – Silesian Unit; 5 – Sub-Silesian Unit; 6 – Skole Unit; 7 – Stebnice Unit; 8 – Miocene deposits upon the Carpathians; 9 – Zgłobice Unit; 10 – Miocene deposits of the Carpathian Foredeep; 11 – location of exotics

The boring activity of foraminifers have been recorded during taxonomical studies on scleractinian corals derived from many exotics, coming from the Skole, Sub-Silesian, and Silesian nappes (Fig. 1). The geographical and geological position of the material illustrated in this paper is as follows (lithostratigraphical names and age of deposits where exotics were found are given in the brackets); Sub-Silesian Nappe: 1. Jastrzębia near Lanckorona (Grodziszcze Conglomerates, lower Aptian), 2. Woźniki near Wadowice; 3. Krzywica near Mogilany (Verovice Beds, Hauterivianlower Aptian); Silesian Nappe: Leńcze near Kalwaria Zebrzydowska (Istebna Beds, Senonian), Gródek nad Dunajcem near Nowy Sącz (Ciężkowice Beds, Eocene); Skole Nappe: Lipnik Hill near Przemyśl (Ropianka Formation, Maastrichtian—Paleocene).

# ENCRUSTING FORAMINIFERA Lithocodium aggregatum

The boring foraminifers belonging to *Troglotella incrustans* Wernli & Fookes, 1992 in the studied material occur in close association with the encruster foraminifera *Lithocodium aggregatum* Elliot, 1956.

Lithocodium Elliot, 1956, monospecific genus, is common in calcareous, well oxygenated, fully marine sediments of Mesozoic age in the Tethys. Possible palaeodepths of abundant specimens range between ca. 15–60 m b. s. l. It is not known from more boreal or austral deposits and has never been found in any argillaceous rocks (Banner et al., 1990). The taxonomical affinity of Lithocodium has been a subject of differing interpretations. Many authors attributed Lithocodium to the green algae from the family Codiaceae. It has also been regarded as a hydrozoan, stromatoporoid, red algae, lichen, or as a cyanobacterial structure (for review see Leinfelder, 1986; Banner et al., 1990; Schmid & Leinfelder, 1996). The foraminiferal nature of this organism is accepted here. This interpretation of Lithocodium was as-

sumed by Schmid and Leinfelder (1995) and is presented in detail in their paper published in 1996. Detailed list of synonyms of this taxon is given by Schmid (1996). According to Schmid and Leinfelder (1996), the features of Lithocodium which point to its foraminiferal nature are following: the partial coiling of the test, microglanular, imperforate wall with alveoli, the ability to agglutinate particles and the facultative occurrence of phrenotheca-like structures. The agglutinating abilities of Lithocodium excludes its codiacean nature. Lithocodium was included by them to the order Lituolida, superfamily Loftusiacea, family Cyclamminidae, subfamily Choffatellinae. Radially arranged alveolar structures are covered by a thin outer layer similar to loftusiid foraminifera such as Pseudocyclammina. The internal cavities of Lithocodium represent the foraminiferal chambers. Schmid and Leinfelder (1996) suggest that alveoli of test of Lithocodium may have been the site of photoautothrophic symbionts. The existence of such a symbiotic association is suggested by the fact that Lithocodium occurs in shallow marine carbonates. According to Leinfelder et al. (1993) Lithocodium can be an useful environmental indicator in carbonates of controversial bathymetry and indicates shallow marine environment of normal salinity and moderate and high energy waters.

Schmid and Leinfelder (1996) belived that the *Lithocodium aggregatum* and the microploblematicum *Bacinella* Radoicic, 1959 are two different taxa. Some authors (e.g., Segoznac & Marin, 1972; Maurin *et al.*, 1985; Banner *et al.*, 1990; Neuweiler & Reitner, 1992) also included in *Lithocodium* the irregular meshwork structures of *Bacinella*. *Lithocodium* and *Bacinella* often occur in association, and for this reason both structures can be interpreted as tissue differentiation or different ecological varieties. The chambers of *Lithocodium* can be crossed by phreonothecal-like structures, which causes *Lithocodium* locally to show "bacinellimorph" fashion (Schmid & Leinfelder, 1996). Because of difficulties in the contradinstinction of both taxa, many authors describe them as *Lithocodium/Bacinella* structures.

According to Leinfelder *et al.* (1993), there are some differences in the palaeoecological distribution of both forms. *Bacinella* may still occur in slightly more restricted shallowwater settings, where *Lithocodium* is rare or absent.

## DESCRIPTION OF THE Lithocodium-Troglotella ASSOCIATION

External surfaces of skeletal elements, mainly scleractinian coral skeletons (which have been studied in detail), are often encrusted by *Lithocodium*. In the places where it has grown into the interseptal space of the coral skeleton it sometimes shows "bacinellimorph" shape (Fig. 2G). Tests of the foraminifera *Troglotella incrustans* ("bubble-like structures") often occur inside chambers of *Lithocodium* (Fig. 2A, B). The shape of tests is irregular, depending on the orientation of thin sections and the internal outline of *Lithocodium* chambers. Lager single cavities may be inhabited by more then one individual of *Troglotella* (Fig. 2B). The interiors of tests can be infilled by micrite (Fig. 2F).

Troglotella facultatively lived inside chambers of Lithocodium or bored into the carbonate skeletal substrate encrusted by it. Tests are sometimes visible in the borings (Fig. 2C-E). However more often borings clearly referred to Lithocodium chambers, but tests of Troglotella are not present there (Fig. 2G, H, J). Locally on 5 mm of carbonate skeletal substrate 10–15 more or less distinguishable borings which appear to be produced by these foraminifers have been found.

Usually, skeletal substrate encrusted by *Lithocodium* is clearly eroded but particular borings can not be distinguishable (Fig. 2J). Tests of *Troglotella* are visible sometimes on such bored surfaces (Fig. 2F), which clearly differ from surfaces without encrustation or encrusted by organisms other then *Lithocodium* and *Bacinella* (cf. Fig. 2I, J). It makes it easier to distinguish of *Lithocodium* if its thickness is small or it is badly preserved.

Locally, fine, filamentous tunnelings infilled by micrite are visible beneath the *Lithocodium*/substrate contact (Fig. 2H). Occurence of *Troglotella* outside of the association with *Lithocodium* is uncertain (Fig. 3).

In the studied material *Bacinella* is much less common then *Lithocodium*. Tissue differentiation of *Lithocodium* causes that it is sometimes difficult to distinguish both organisms. Locally, in the skeletal elements encrusted by *Bacinella* fine microborings are visible (Fig. 4).

## **DISCUSSION**

The association of both foraminifers presented above was described for the first time by Leinfelder *et al.* (1993) from the Upper Jurassic of Portugal, Spain and southern Germany. Detailed description and discussion of this association is given by Schmid and Leinfelder (1996), where interpretation of *Lithocodium* as a foraminifera is also presented. Leinfelder (1989; see in Schmid & Leinfelder, 1996; p. 35) was the first who identified bubble-like structures within cavities of *Lithocodium* as foraminiferal tests. These

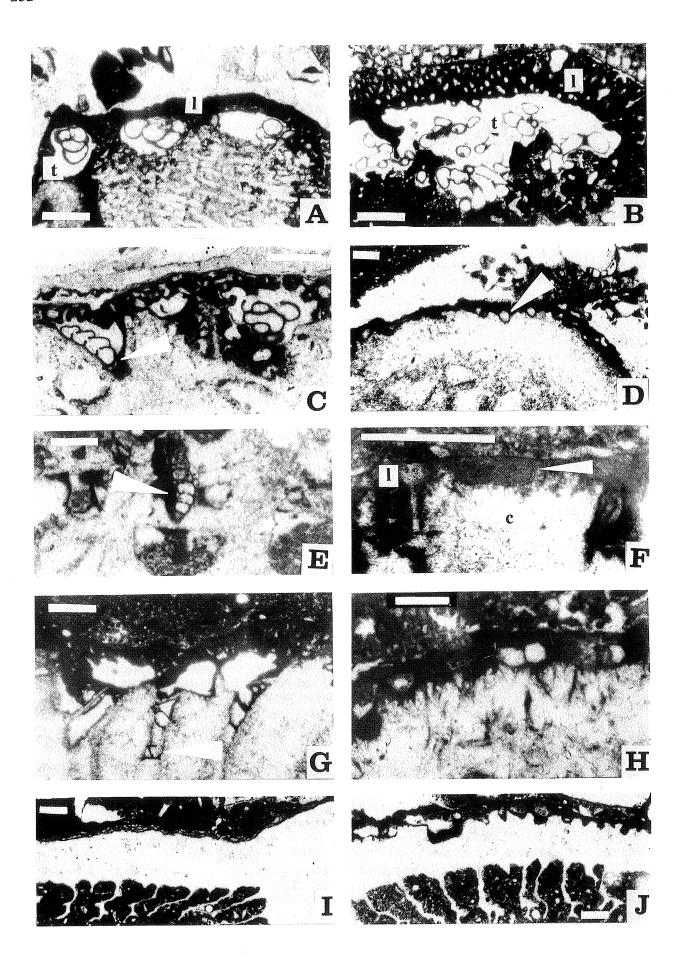
structures were earlier regarded as calcified sporangia or skeletal elements of Lithocodium and have even been a reason for determination of new taxa: Lithocodium japonicum and L. morikawai by Endo (1961) and Bacinella crispa by Eliášová (1981). Leinfelder et al. (1993) determined the foraminifera lived in association with Lithocodium as Bullopora aff. laevis. Such taxonomical assignation was also assumed by the present author in a preliminary note about boring foraminifera from the Štramberk-type limestones (Kołodziej, 1995). According to Schmid and Leinfelder (1995, 1996) this foraminifera should be attributed to Troglotella incrustans. This genus and species was described by Wernli and Fookes (1992) from reef facies of the upper Kimmeridgian in Saint Germain-de-Joux, Eastern France. Also in the opinion of Fookes (1995) foraminifers associated with Lithocodium and described by Leinfelder et al. (1993) should be assigned to Troglotella incrustans. Schmid and Leinfelder (1996) gave emended diagnosis for the Lithocadium and attributed it to the superfamily Hormosinacea, family Telamminidae. The emended diagnosis includes the boring behaviour of this foraminifera. Wernli and Fookes (1992), and Fookes (1995) mentioned Lithocodium aggregatum among organisms occurring with Troglotella but either text or figures do not indicate that these organisms lived in close association. However, E. Fookes (personal communication, 1996) had recorded in his material some examples Lithocodium-Troglotella association. In his opinion there is also possibility that in the samples derived from high energy areas Lithocodium could be eroded.

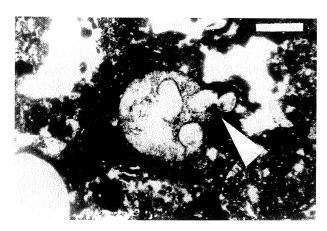
According to Cherchi et al. (1995), the foraminifera described by Leinfelder et al. (1993) as Bullopora aff. laevis is Troglotella incrustans, but does not display boring activity. Moreover, these authors believed that structures within cavities of Lithocodium are not foraminifera, but could be produced by other endolithic organism or by Lithocodium itself. However, such an interpretation could be only possible due to these authors did not know the new results presented by Schmid and Leinfelder (1995, 1996).

## Life cycle and character of association

Schmid and Leinfelder (1996) assumed that the co-occurrence of both foraminifers was a life association. Some arguments in their opinion exclude the post-mortem infestation of Lithocodium by Troglotella. Even in thick, multilayered Lithocodium, most chambers were inhabited by Troglotella, which is most unlikely in the case infestation was post-mortem. The imperforate nature of the Lithocodium wall would hinder both settlement paths for zygotes of Troglotella and nutrient-rich waters. Phrenotheca-like structures crossing the chambers of Lithocodium are rare in the Upper Jurassic, when the association of both foraminifers is common, suggesting that chambers were occupied by Troglotella. On the other hand, there is no reason why Lithocodium should overgrow a test of dead foraminifers. Besides, the irregular shape of tests inside chambers of Lithocodium shows that Troglotella grew up in a restricted space.

In the studied material *Lithocodium* grows into borings made by *Troglotella* (Fig. 2G), which also seems to confirm the life association of both foraminifers. However, micrite infilling the tests of *Troglotella* (Fig. 2F) should be inter-





**Fig. 3.** Small skeletal element bored by ?*Troglotella* not associated with *Lithocodium*; Leńcze. Scale bar = 0.5 mm

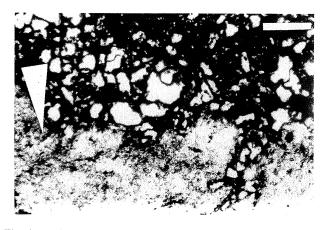


Fig. 4. Fine microborings (arrows) in skeletal element encrusted by Bacinella; Gródek nad Dunajcem. Scale bar = 0.5 mm

preted rather as micrite cement and not skeletal automicrite of *Lithocodium*.

The following stages in the life cycle of *Troglotella* are suggested by Schmid and Leinfelder (1996):

- 1. Infestation of *Lithocodium*. Gametes of *Troglotella* settled on the ectoplasma of *Lithocodium* were transported into the endoplasma.
- 2. Early growth stage. *Troglotella* attached itself to the roof of chambers or the *Lithocodium* substrate. Usually an early boring stage is present.
- 3. Later growth stages. Epibenthic growth stages. Authors suggest that *Troglotella* fed on the supposed photoauthotropic symbionts of *Lithocodium* or their synthesized products.
- 4. Reproduction. Propagation of *Troglotella* during asexual reproduction of *Lithocodium*. The exact character of this symbiotic association (mutualism, commensalism, parasitism) is difficult to evaluate, because fitness data can not be obtained from fossils. Then, it is useful to use the term "symbiosis" in its broad, previous sense. At present most specialists use such a meaning of this term (e.g., Ahmadjian & Paracer, 1986).

According to Schmid and Leinfelder (1996) the *Litho-codium-Troglotella* association could have a commensalic character, with possibly slightly parasitic nature. The *Troglotella* possibly fed autotrophic symbionts of *Lithocodium* or their synthesized products.

The *Lithocodium-Troglotella* association has not close fossil or Recent analogs, which additionally makes it difficult to assess the nature of this association. Symbiotic associations between foraminifera and other organisms (besides autosymbiotic algae) are also rare. Kaźmierczak (1973) re-

corded the commensalistic foraminifera *Tolypammina vagans* (Brady, 1879) inhabited the water system of Oxfordian siliceous sponges. Foraminifers fed off nourishment taken in by sponges, and used particles of sediment that got there for building their tests.

#### Mechanism and role of bioerosion

Wernli and Fookes (1992) determined *Troglotella incrustans* as a foraminifera which lived within pre-existing microcavities (see also Fookes, 1995). The studied material confirms borings and not the calcivacicole life habit of this foraminifera (Leinfelder *et al.*, 1993; Schmid & Leifender, 1995, 1996).

According to Leinfelder et al. (1993) foraminifera bored in a juvenile stage and encrusted the surface of cavities in Lithocodium during the adult stage. Borings are perpendicular to the substrate. In the studied material, tests of Troglotella often are not present in the borings, but shape of chamber of Lithocodium clearly fit in the borings (Fig. 2G, H, J). This may suggest mobility of this foraminifera in time of boring or simply tests are not preserved. Most borings recovered in the studied material differ from the pattern described by cited authors. Borings perpendicular to the substrate are rare (Fig. 2E). Bored surfaces of skeletal elements are irregular, often without distinct distinguishable borings (Fig. 2J). Tests of Troglotella although very rary, are visible on bored surfaces suggesting that borings were made by this foraminifera, and *Lithocodium* only grew into these borings. However it is possible that *Lithocodium* could produce fine, filamentous microborings (Fig. 2H). Similar outgrowths were described by other authors both in fossil and modern examples, and are regarded as pseudopodial tunnelling (e.g.,

Fig. 2. (A, B) Troglotella incrustans (t) inside of Lithocodium aggregatum (1) chambers; (C, D, E) Coral encrusted by Lithocodium and bored by Troglotella (arrows); (F) Bored coral septum (c). External part of Lithocodium (l) is eroded; test of Troglotella (arrow) is infilled by micrite; (G) Bored surface of coral skeleton below Lithocodium encrustation. Arrow shows "bacinnelimorph" fashion of Lithocodium. Borings clearly referred to Lithocodium chambers, but tests of Troglotella is are not present; (H) Fine microborings within coral skeleton encrusted by Lithocodium; (I) Corallite encrusted by Koskinobullina socialis; (J) This same corallite, but clearly bored below encrustation of Lithocodium. Tests of Troglotella are not preserved. A, D, E, I – Krzywica; B – Gródek nad Dunajcem; C, J – Lipnik Hill; F, G, H – Leńcze. Scale bars = 0.5 mm

Poag, 1969; Mateucci, 1980; Plewes *et al.*, 1993). Authors describing modern boring foraminifera speculated that boring may be accomplished by pseudopodia through chemical dissolution (Poag, 1969).

The potential advantages of bioeroding mode of life, summarized by Vénec-Peyré (1996), are nutrion, test building and protection. Many authors suggest that the purpose of penetration in substrate is protection against abrasion and predators (e.g., DeLaca & Lipps, 1972; Vénec-Peyré, 1987; Plewes et al. 1993). Such an interpretation can be good explanation of boring behaviour for *Troglotella* living outside of *Lithocodium*. Adaptation to coelebiontic style of life of adult forms could be also profitable for living in exposed environment. In the material studied by Fookes (1995) with the exception of *Troglotella incrustans* and "*Tubiphytes*" morronensis, foraminifers are rarely found in the reef complex. According to Fookes the adaptive strategy (living in pre-existing cavities) during ontogeny allows the colonization of a higher energy environment by *Troglotella incrustans*.

Another explanation of boring behaviour is obtaining material required for test construction. Todd (1965) speculated that modern *Rosalina carnivora* sought calcium carbonate for test building. Such an advantage of boring behavior was also supposed by Vénec-Peyré (1987). It is also possible that boring foraminifers obtained some food from organic matter in the skeletal substrate or endolithic microflora (Plewes *et al.* 1993; Matteucci, 1980).

Troglotella most probably bored into skeletons of dead organisms. Alexander and DeLaca (1987) described the case of modern species *Cibicides refulgens* which obtain nutrients from the living host (scallops) by the erosion of the shell beneath the place of attachment of its test. A similar habit was proposed for fossil boring foraminifera by Banner (1971) and Baumfalk *et al.*, (1982).

In the studied material borings made by foraminifera are restricted to the external part of skeletal elements (mainly corals). Smyth (1988) showed that modern *Cymbaloporella tabellaeformis* bores into the outer shell surface of gastropods. She assumed, that this is probably because most foraminifera are positively phototrophic. According to Schmid and Leinfelder (1996), it is possible that *Lithocodium* lived with photoautothrophic symbionts.

In the material studied by the present author 10-15 borings can be recognized on 5 mm of coral skeleton (Fig. 2J). Smyth (1988) stated from 1 to 74 borings per shell (having length 13-30 mm), and infection rate was 8.4%. Vénec-Peyré (1985) reported that 150 000-250 000 individuals of bioeroding foraminifers on 1-2 m occur in bioclast on the back-reef area and outer slopes of Moorea Island. Other quantitative data, not numerous however, are summarized by Vénec-Peyré (1996). The role of foraminifera in bioerosion is not well recognized. Most researches of bioerosion do not take into consideration the foraminifers. However, both fossils and recent examples show that foraminifera do take part in the weaking and subsequent breakdown of skeletal grains and consequently contribute to the production of detritus and silt-sized particles. Their role in bioerosion has been overlooked owning due to the small size of foraminifera. The bioeroding activity of foraminifera

causes that substrate is more vulnerable to other process of erosion (Vénec-Peyré, 1987, 1993, 1996). The importance of foraminifera as a member of a destructing guild may be much more larger then is currently estimated based on examples mentioned in literature. Some rosette microborings attributed to the activity of algae may be produced by foraminifera (Plewes *et al.*, 1993). A similar assumption was given by Cherchi and Schroeder (1991). However, it is possible that the borings described by these latter authors were not produced by foraminifera, which were only secondary nestlers (Plewes *et al.*, 1993).

The studied material suggests boring behaviour of Bacinella. According to Maurin et al. (1985) "bacinellid textures" are microbial nature and had boring potential, as attested by communicative in rudistid shells, infilled with micrite or tiny bacinellid fabrics in continuity with outer and inner encrustings. Boring activity of Bacinella is also mentioned by Neuweiler and Reitner (1992) and Arias et al. (1995), but most authors do not mention such activity of Bacinella. However, the lack uniformity in understanding of Bacinella and lack of well documented material make impossible verification nature of the borings described in the citated papers. The boring activity of Bacinella certainly is a topic for further studies. However, the material from the Štramberk-type limestones is insufficient for such studies. If within bacinellid structures Troglotella is not present, this could be additional an argument for the separation such structures from Lithocodium.

#### Stratigraphical distribution

The Lithocodium-Troglotella association does not occur throughout whole range of Lithocodium, which is from Anisian to Cenomanian/?Turonian (Schmid & Leinfelder, 1996). According to Moussavian (1992), Lithocodium/Bacinella still occurs in Campanian/? Maastrichtian deposits, but photographs presented by him do not allow verification. Up to now, Troglotella and the Lithocodium-Troglotella association was described from Upper Jurassic shallow-water, mostly reefal deposits. The list of synonyms of Troglotella incrustans (associated with Lithocodium or not) is given by Schmid and Leinfelder (1996). These authors noticed that the Lithocodium-Troglotella association occurs also in the Štramberk Limestone from Moravia (Eliášová, 1981; pl. II, fig. 2), which they assumed to the Tithonian. However, the stratigraphical range of these deposits has extended to the lower Berriasian (Houša, 1990; Eliáš & Vašiček, 1995). Previous data suggest that the association is not restricted to the Upper Jurassic and Berriasian. Endolithic foraminifera resembling Troglotella and bubble-like structures within Lithocodium crust can be seen in paper of Neuweiler (1995, pl. 26, fig. 7; pl. 56, fig. 4) dealing with Aptian/Albian mud mounds from N Spain. Such structures, presumably tests of Troglotella associated with Lithocodium are often in that material (F. Neuweiler, personal communication, 1996). Schlagintweit (1991; pl. 10, figs. 13-14), describing upper Aptian rudistid limestones of the Northern Calcareous Alps illustrated boring foraminifera resembling Troglotella incrustans (D. U. Schmid, personal communication, 1996). In this material most often boring foraminifera are not associated with Lithocodium, but an association of both foraminifers is also present (F. Schlegintweit, *personal communication*, 1996). It is difficult to say whether structures visible inside of chambers of *Lithocodium* from the Upper Albian of Spain (see Cherchi *et al.*, 1995, pl. II) represent foraminiferal tests, or are only normally developed phrenothecalike structures.

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#### Streszczenie

### DRĄŻĄCE OTWORNICE Z WAPIENI EGZOTYKOWYCH TYPU SZTRAMBERSKIEGO (TYTON–DOLNY BERIAS, KARPATY)

#### Bogusław Kołodziej

W wapieniach egzotykowych typu sztramberskiego (tytondolny berias) z polskich Karpat fliszowych (Fig. 1) stwierdzono

liczne występowanie drążących otwornic z gatunku Troglotella incrustans Wernli & Fookes, 1992. Występują one w ścisłej asocjacji z organizmem inkrustującym Lithocodium aggregatum Elliot, 1956. Autor zgadza się z interpretacją przedstawioną przez Schmida i Leinfeldera (1996), że takson ten należy zaliczyć do Foraminiferida. Troglotella drążyła podłoże szkieletowe (badano głównie szkielety koralowców) inkrustowane przez Lithocodium (Fig. 2C-F) lub żyła w komorach Lithocodium (Fig. 2A, B). Pojedyncza komora Lithocodium mogła być zamieszkana przez więcej niż jednego osobnika Troglotella (Fig. 2B). Na 5 mm podłoża szkieletowego można miejscami stwierdzić ok. 10-15 bardziej lub mniej wyodrębniających się drążeń (Fig. 2J). W obrębie inkrustowanego podłoża występują również drobne, filamentowe drążenia (Fig. 2H). Powierzchnie elementów szkieletowych inkrustoweane przez Lithocodium i drażone przez Troglotella wyraźnie kontrastują z powierzchniami pozbawionymi inkrustacji lub inkrustowanymi przez inne organizmy (cf. Fig. 2I, J. Skorupki Troglotella często nie są zachowane w wydrążeniach (Fig. 2G, J). Występowanie tej otwornicy poza asocjacją z Lithocodium jest niepewne (Fig. 3).

Współwystępowanie obu otwornic po raz pierwszy opisano z osadów oksfordu i kimerydu Portugalii, Hiszpanii i południowych Niemiec (Leinfelder et al., 1993) oraz przeanalizowano przez Schmida i Leinfeldera (1996). Pęcherzykowate struktury w komorach Lithocodium uważane były wcześniej za jego element szkieletowy. Wernli i Fookes (1992) uważali, że Troglotella żyła w istniejących zagłębieniach. Na podstawie badanego materiału można stwierdzić drążący tryb życia tej otwornicy oraz symbiotyczny (w szerokim znaczeniu) charakter jej współwystępowania z Lithocodium (Schmid & Leinfelder, 1996). Brak współczesnego odpowiednika dyskutowanej asocjacji otwornic utrudnia jednak dokładne określenie jej charakteru. Korzyści jakie mogła odnosić Troglotella z drążącego trybu życia to możliwość zasiedlania wysokonergetycznych środowisk, ochrona przed drapieżnikami lub możliwość uzyskiwania materiału do budowy skorupek (Vénec-Peyré, 1996). Dyskutowana asocjacja była dotychczas opisywana z górnej jury, jednak nowe dane z innych obszarów sugerują, że jej zasięg stratygraficzny należy rozszerszyć do albu.

Przypadki zarówno współczesnych jak i kopalnych otwornic drążących są nieliczne. Znanych jest zaledwie około 20 gatunków takich otwornic, głównie współczesnych i trzeciorzędowych. Jednak znaczenie otwornic w bioerozji mogło być znacznie większe niż można to szacować na podstawie znanych przykładów. Niektóre mikrodrążenia przypisywane zwykle glonom mogły być wykonane przez otwornice.

W badanym materiale stwierdzno również mikrodrążenia w elementach szkieletowych inkrustowanych przez problematyczny organizm *Bacinella irregularis*, który część autorów uważa za synonim *Lithocodium aggregatum* (Fig. 4).