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Photosynthetic activity in Devonian Foraminifera

Zofia Dubicka[1,2], Maria Gajewska[1], Wojciech Kozłowski[1], Pamela Hallock[3], Johann Hohenegger[4]

[1]Faculty of Geology, University of Warsaw, Warsaw, Poland
[2]Ecological Chemistry, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany
[3]College of Marine Science, University of South Florida, St. Petersburg, USA
[4]Department of Palaeontology, Universität Wien, Wien, Austria

Correspondence to: Maria Gajewska (mi.gajewska@uw.edu.pl)

Abstract. Photosynthetically-active foraminifera are important carbonate producers contributing nearly 5% of the reef and nearly 1% of the total global calcium carbonate budgets. The abilities to be photosynthetically active, foraminifera realize by endosymbiosis with microalgae or by sequestering plastids (kleptoplasts) of digested algae. These ecological behaviors are a great advantage for the continued growth, survival of the hosts and enhance of foraminiferal calcification. Our data provide concurrent pieces of evidence for, as of now, the earliest (mid-Devonian) photosymbiosis in protists observed in first true advanced multichambered calcareous foraminifera *Semitextularia* from the tropical shelf of the Laurussia paleocontinent. This adaptation might have had a significant impact on the evolutionary radiation of calcareous Foraminifera in the Devonian ("Givetian revolution"), which was one of the most important evolutionary events in foraminiferal history. The observed phenomenon coincided with the worldwide development of diverse calcifying marine communities inhabiting shelf environments linked with Devonian stromatoporoid-coral reefs.

1 Introduction

Among photosynthetically-active protists, symbiont-bearing benthic Foraminifera (SBBF), which compose less than 10% of all living families (Lee and Anderson, 1991), are important carbonate producers (Prazeres and Renema, 2019) contributing nearly 1% of the total global calcium carbonate budgets (Hohenegger, 2006; Langer, 1979). The occurrence of modern SBBF is limited to tropical and warm temperate zones and is related to the light requirements of the hosted symbiotic microalgae (Renema, 2018). Living in warm, shallow, euphotic environments enables hosts to use their tests as "glass houses" suitable for the husbandry of endosymbiotic algae (Hohenegger, 2009). Hence, SBBF inhabit mainly upper euphotic shallow-reef and lagoon environments; however, some groups hosting diatoms can be found along reef slopes in transparent water down to 130 m depth of the lower euphotic zone (Hohenegger, 2000). This ability is a great ecological advantage (Lee et al., 2010; Schmidt et al., 2004) as through photosynthesis, endosymbionts provide their hosts with the energy for much of their metabolic needs (i.e., mixotrophy; Hallock, 1981; Selose et al., 2017) and can also enhance the process of foraminiferal calcification (Hallock, 1999; McConnaughey, 1997; ter Kuile, 1991). The most important benefits for the symbionts are protection afforded by the host tests (Hohenegger, 2000, 2018) and uptake of inorganic nutrients from host metabolites (Hallock, 1999).

Apart from endosymbiosis, another ecological adaptation that enables foraminifers to be photosynthetically active is by kleptoplasty (Cesbron et al., 2017; Goldstein et al., 2004; Pillet et al., 2011). Foraminifers sequester plastids from microalgal prey (e.g., diatoms), and those plastids can remain photosynthetically active for days to weeks within the foraminifera (Jauffrais et al., 2016, 2018). Products of photosynthesis, such as glucose, can be especially important during periods of food scarcity. In dysphotic and aphotic habitats like the deeper bathyal benthos, sequestered plastids that originate from planktic diatoms can assimilate inorganic carbon, nitrate and sulfur (Jaufrais et al., 2019). Feeding upon microalgae, and harvesting and maintaining active plastids, is an evolutionarily more direct way to function as a mixotrophic organism compared to the more complicated array of adaptations associated with obligate symbioses.

Considering the important roles played by SBBF and kleptoplastic foraminifers in carbonate production of present coral reefs and shallow-marine ecosystems (Baccaert, 1986; Fujita and Fujimura, 2008; Prazeres and Renema, 2019), as well as the advantage of endoplasmic photosynthesis in foraminiferal evolution, we are seeking the first evidence of photosynthetic activity in foraminifers in the past. Presumptive candidates are the first multi-chambered calcareous foraminifers with leaf-like tests such as *Semitextularia* (Eifelian–Frasnian), which are morphological counterparts to some recent SBBF (Figs. 1, 2). Semitextulariids were globally distributed on Devonian inner shelves, shallow-marine, well-illuminated habitats such as tropical reefs and lagoons (see Table S1). They and other well-known Devonian groups such as Nanicellidae and Eonodosariidae died out following the Kellwasser event of the Frasnian–Famennian crisis (Vachard et al., 2010) that triggered the rapid collapse of the prolific stromatoporoid-coral reef ecosystems. In principle, the origin of *Semitextularia* occurred at the beginning of the Middle Devonian foraminiferal radiation, which is the so-called "Givetian revolution" (Vachard et al., 2014) and is considered to be the most important Paleozoic evolutionary event for these protists. This event is associated with 'the replacement of the primitive agglutinated wall of the Textulariata by the more advanced secreted wall of the Fusulinata' (Vachard et al., 2014).

In this paper, we hypothesize that the Devonian semitextularids were not only among the first true multi-chambered calcareous foraminifers, but may also have been the first algal symbiont-bearing or chloroplast-sequestering foraminifers. To test this hypothesis, we compared paleo-populations of *Semitextularia* derived from facies of coeval horizons (upper Eifelian, Middle Devonian; Skały Beds, HCM, Central Poland) characterized by contrasting paleo-depths with different levels of light intensity representing the tropical southern shelf of the Laurussia paleo-continent (Szulczewski, 1995). Samples were compared in terms of a possible photosynthesis-related microhabitat effect recorded in the carbon-isotopic data, since photosynthesis by algal symbionts of modern larger benthic foraminifers has a significant impact on $\delta^{13}C$ composition. Enrichment of ^{13}C in the microenvironment occurs when $^{12}CO_2$ is sequestered by algae during photosynthesis (Ravelo and Hillaire-Marcel, 2007). Moreover, our findings are supported by ecological similarities and a functional-morphological comparison between *Semitextularia* and recent SBBF.

2 Materials and Methods

The studied samples were collected in the lower part of the Skały Formation (upper Eifelian–lower Givetian) outcrop in the Holy Cross Mountains inlier (HCM, Central Poland). The Skały Formation represents an epicratonic facies of the southern (so-called Fennosarmatian) tropical shelf of the Laurussia paleocontinent (Szulczewski, 1995) close to the northern part of the East European Platform (referred to as the Łysogóry unit) located in the HCM. The Skały outcrop (50°53'044.69"N 21°9'33.75"E) is part of the well-known Grzegorzowice-Skały (G-S) succession exposed along the Dobruchna brook (Pajchlowa, 1957; Zeuschner, 1869), which is a key section for the Devonian of the Łysogóry facies region (Szulczewski, 1995). The Miłoszów outcrop (50°54'09.5"N 21°07'14.5"E; Samosonowicz, 1936), located 3 km west of Skały, complements the key succession by virtue of the closely-correlated Miłoszów limestone complex (see faunal-summary tables in Biernat, 1966; Pajchlowa, 1957; Stasińska, 1958), which was recently exposed in Skały. For detailed geological, stratigraphic, and sedimentary environment background, see Supplement Discussion/Note).

We examined a total of 25 samples from the upper Eifelian (Middle Devonian) Skały beds of the Holy Cross Mountains in Central Poland. The specimens studied were Semitextularia thomasi Miller and Carmer, including the isotopic signatures of the tests and the enclosing rock matrix. The latter included: (1) a marly intercalation in Miłoszów coral-bearing biostromes (two intervals Miłoszów 11 and 12), representing an upper euphotic (well-illuminated) environment (10 samples); (2) Skały brachiopod shales (SBS), containing a mesophotic (lower euphotic) coral assemblage (Skały 11and A+11A/Skały brachiopod shales, 14 samples); and (3) marls with abundant solitary corals (Skały C sample), representing a proximal forereef environment characterized by intermediate photic conditions. All samples were derived from very soft marly clays with low permeability and very low paleoheating rate (Dubicka et al., in press), that ensured favorable conditions for excellent fossil preservation. Very well-preserved, three-dimensional specimens, with no sediment or mineral infillings, with original lamellar test microstructure, and with no evidence of any dissolution or recrystallization, were analyzed (Narkiewicz and Malec, 2005). Lack of diagenetic alternation of the Skały samples can be additionally supported by uniquely preserved brachiopods with preserved brachidia, primary shell structures (Biernat, 1966), and in some cases also relicts of the original color pattern (Biernat, 1984). Also, the porous stereom of crinoids includes original (metastable) high-Mg calcite, which is the first phase to be affected during the diagenetic alteration of calcareous fossils (Gorzelak et al., 2011).

During maceration, samples were mechanically disintegrated (crumbled into ca. 1–2 cm3 pieces), dried and repeatedly soaked in water and detergent, then heated and dried again following decantation. To intensify the rock disintegration process, some samples were also subjected to a maceration technique using Rewoquat (Jarochowska et al., 2013). After being washed in an ultrasonic cleaner, the residuum was sieved using a mesh size of 0.053 mm. From the residue, foraminifera were hand-picked and studied using a Nikon SMZ 18 stereoscopic microscope. More detailed taxonomic observations and photographic documentation were made using a Zeiss Sigma VP scanning electron microscope at the Faculty of Geology, University of Warsaw.

For oxygen and carbon isotopic analyses, 35 foraminiferal samples and 25 bulk-rock samples were prepared. Foraminifera were manually chosen from the residue prior to undergoing multiple additional cleanings in an ultrasonic cleaner. Sediment-free Semitextularia thomasi Miller and Carmer specimens were placed in Eppendorf tubes (ca. 10 large adult specimens in each tube). Bulk rock samples were prepared by grinding a portion of rock material of ca. 2 g to powder using a mortar. The isotopic analysis was performed at the GeoZentrum at the University of Erlangen, Germany. Samples were reacted with 100% phosphoric acid at 70ºC using a Gasbench II connected to a Thermo Fisher Delta V Plus mass spectrometer. Reproducibility of the analyses was 0.06 and 0.06‰ (±1 s.d.) for δ18O and δ13C values of laboratory standard Sol 2 (n = 16) and 0.07 and 0.06 ‰ (±1 s.d.) for δ18O and δ13C values of laboratory standard Erl 5 (n = 22), respectively. All isotopic data are reported in per mil relative to the VPDB scale and presented in Tables S1 and S2 for Miłoszów and Skały, respectively.

All statistical analyses were carried out using the program package PAST 4.02 (Hammer et al., 2001).

3 Results

3.1 Morphometrics of the *Semitextularia* tests

Differences in test morphology of *Semitextularia* between specimens from Miłoszów, representing an upper euphotic environment (see appendix Discussion), and Skały, interpreted as lower euphotic (i.e., mesophotic) environment (Zapalski et al., 2017), were tested for differences in size and shape. Size represented by *test height* did not differ significantly among samples [ANOVA: $p(H_0) = 0.499$; Tables S2, S3], followed by pairwise comparisons. Only specimens from Skały 1 were, on average, slightly smaller compared to the other samples. Shape, represented by the size-independent parameters $\sqrt{area}/height$ and $width/height$, also did not differ among samples [ANOVA; $p(H_0) = 0.697$, $p(H_0) = 0.122$; Table S4], again with some smaller $width/height$ ratios for Skały 1. The complete overlapping of samples is supported by regression functions of *test area* to *test height* (Fig. 3).

3.2 δ^{13}C and δ^{18}O values in Devonian foraminiferal shells along with rock matrix samples

Carbon isotopic data from *Semitextularia* specimens, as well as from bulk-rock samples were compared (Tables S5, S6). For *Semitextularia*, δ^{13}C-values were significantly higher in specimens from Miłoszów (2.86, 2.71) compared to Skały [1.47, 0.84, 1.60; $p(H_0) = 1.05$E-06]. In contrast, in bulk-rock samples, δ^{13}C-values were significantly lower in Miłoszów (-0.05, -2.24) compared to Skały 11 (1.71) and Skały C (0.96) specimens, with intermediate values in Skały A+11A rock samples [0.10; $p(H_0) = 3.07$E-11].

Oxygen isotopic values in *Semitextularia* tests also resulted in significant differences among samples [$p(H_0) = 3.56$E-08]. Averaged δ^{18}O-values were significantly lower in Miłoszów (-6.35, -6.44) compared to Skały C (-5.68) and Skały A+11A (-5.49), while Skały 11 values fell in between (-5.95). Values for δ^{18}O of bulk-rock samples also differed significantly [$p(H_0) = 9.44$E-08], with Miłoszów samples showing significantly lower values (-6.62, -6.91) compared to Skały 11 (-5.56) and Skały C (-5.43) samples; with values for Skały A+11A samples falling in between (-6.17).

Comparisons among stable-isotopic values of *Semitextularia* specimens and bulk-rock samples differed (table S7). In Miłoszów 11, the δ^{13}C-values in *Semitextularia* (2.86) were much higher than for the bulk-rock sample (-0.05). Similar differences were found at Miłoszów 12, with high values for *Semitextularia* (2.71) compared to the bulk-rock sample (-0.05). Skały samples are quite different from Miłoszów. In both Skały 11 and Skały A+11A, the δ^{13}C-values of bulk-rock samples were significantly higher (both samples 1.71) compared to *Semitextularia* (1.47 in Skały 11, 0.84 in Skały A+11A). At Skały C, however, the carbon isotopes are statistically similar, 1.60 for *Semitextularia* versus 0.96 for bulk rock.

Comparing oxygen-isotopic data between *Semitextularia* and bulk-rock samples produced different results. The δ^{18}O-values do not differ between *Semitextularia* specimens and bulk rock in either Miłoszów sample (table S7). Similar congruence was found in Skały C samples, with δ^{18}O-values of -5.68 for *Semitextularia* specimens and -5.43 for bulk rock. Although oxygen-isotopic values for Skały 11(-5.95 for *Semitextularia*, -5.56 for bulk rock) were similar, because the variance in both groups was extremely low (0.003, 0.005), the differences were significant. In contrast, the δ^{18}O-values of *Semitextularia* specimens (-5.49) and bulk-rock samples (0.10) from Skały A+11A were very different.

Comparisons of δ^{13}C and δ^{18}O values based on foraminifers and bulk-rock samples are shown as scatter diagrams for Miłoszów and Skały samples (Fig. 4).

4 Discussion

The ^{13}C enrichment of *Semitextularia* foraminiferal tests compared to the associated bulk rock (matrix) was interpreted as related to the fractionation of isotopes due to photosynthetic activity in foraminifers that either hosted photosynthetic endosymbionts or were kleptoplastic. This hypothesis is based on previous observations that intracellular photosynthesis influences the δ^{13}C of foraminiferal tests (Ravelo and Fairbanks, 1995; Wefer et al., 1981, 1991). Fractionation of carbon isotopes during photosynthesis can produce δ^{13}C differences between foraminiferal tests and the $\delta^{13}C_{DIC}$ of the ambient seawater in which the foraminifers live, as it strongly influences the foraminiferal microenvironment, i.e., the “internal carbon pool” (ICP) (Ravelo and Hillaire-Marcel, 2007, Wefer et al., 1991; Zeebe et al., 1999). The probability that *Semitextularia* was photosynthetically active is supported by the apparently optically-transparent lamellar test structure (Fig. 1 h–j) that enabled light penetration (Dubicka et al., in press). Furthermore, the test morphology of *Semitextularia* is comparable to representatives of some smaller SBBF to the point that *Semitextularia* seems to be the fossil morphological counterpart of peneroplids. Specimens of both foraminiferal taxa can be characterized by fan-like, bilaterally flat tests with a high surface-to-volume ratio (Hohenegger, 2009), and multiple apertures forming a series of small holes along the entire last chamber. This kind of test represents a way to increase the surface area allowing more symbionts/plastids to be positioned just beneath the test wall to gather light (Haynes, 1965), while multiple apertures are morphological adaptations to resist hydrodynamic forces by strengthening attachments through bundles of pseudopodia, as exemplified by the *Peneroplis* life strategy (Hohenegger, 2011). Specifically, peneroplids hide in the uppermost layer of sand grains or fix with a net of pseudopods to algal filaments (Fig. 2b; Hohenegger, 2009, 2011).

However, differences in δ^{13}C values in *Semitextularia* compared to the bulk-rock samples are much smaller in Skały A11+A samples than those recorded in specimens from Miłoszów and are very minimal in Skały 11 and Skały C specimens. Therefore, there is no clear evidence for photosynthetic activity in the *Semitextularia* tests from the Skały settings, which likely were characterized by lower light intensities (Zapalski et al., 2017). The paleodepth of Skały is estimated as ca. 30–40 meters (see Supplement Geological Setting), which is within the range of the water depth of Recent mixotrophic foraminifers, primarily those housing diatoms, which did not evolve until the Jurassic (Sims et al., 2006). Species hosting dinoflagellates, chlorophytes or rhodophytes tend to be shallower dwelling, especially in shelf-margin environments with reduced water transparency such as the Florida reef tract (Baker et al., 2009), compared to much clearer oceanic waters (Hohenegger, 2006). Thus, reduced photosynthetic activity at the seafloor at the Skały location was likely related to input of nutrients and fine sediments into the basin, thereby limiting light penetration required for sufficient photosynthetic activity to influence carbon-isotopic ratios in the foraminiferal tests. Light penetration declines exponentially with water depth and so declines rapidly with depth even with relatively small changes in water transparency (Hallock and Schlager, 1986; Hohenegger, 2004).

Another point to discuss is the consistency in test morphology of the studied *Semitextularia* as shown by regression analyses of the *test-width/test height* and $\sqrt{area}/test\ height$ ratios (Fig. 3). These ratios can indicate light requirements when harboring microalgae (Hohenegger, 2004), as has been observed in the surface/volume-ratios of some rotaliids (Röttger and Hallock, 1982) and some porcelanous species whose distributions are well correlated with depth (39, 42). Because light intensities would have been higher in the upper euphotic Miłoszów location compared to the mesophotic Skały sites, one could expect differences in test parameters. For example, in hyaline amphisteginid species characterized by highly transparent lamellar test structure, the maximum test diameters are relatively consistent within their depth range, though their minimum diameters decline with depth (Hallock and Hansen, 1979; Hohenegger et al., 1999; Larsen and Drooger, 1977). In this case, optimal light penetration into the test is facilitated by thinning of the lamellae, which could not be demonstrated for *Semitextularia*.

We suspect that *Semitextularia* was kleptoplastic, maintaining plastids that photosynthesized most actively in the upper euphotic zone. Photosynthetic activity sufficient to influence carbon-isotopic ratios is known to decline with depth in foraminifers with diatom endosymbionts (Hansen and Buchhardt, 1979). Moreover, endosymbiosis is likely a more complex co-evolutionary process, especially obligate photosymbioses in which the host is unable to survive without symbionts. Facultative algal symbioses, which occur in some planktic taxa, are unknown among Recent SBBF (Lee and Anderson , 1991).

The basic life history strategy of the Foraminifera involves alternation of generations (Goldstein, 1997), and can be assumed for *Semitextularia* based both on phylogeny and by the dimorphism apparent in fossilized tests. For example, the initial chambers of the specimen in Figure 1e appears to be much smaller than those of other specimens shown in Figure 1. This difference is consistent with sexually-produced, microspheric individuals, compared to generally more common asexually-produced, megalospheric individuals. As hypothesized in previous studies (Dettmering et al., 1998; Krüger et al., 1996), the transfer of endosymbionts during sexual reproduction is more complicated than transfer during asexual reproduction.

The evolution of foraminiferal lineages characterized by algal endosymbiosis occurred repeatedly and independently numerous times since the late Paleozoic, involving unrelated algal groups as well. Previously, the earliest calcareous foraminifers postulated to host algal endosymbionts were the large, complex fusulinids (BouDagher-Fadel, 2008). A true symbiotic relationship between *Semitextularia* and an algal taxon cannot be ruled out from the observations reported here. Nevertheless, our observations are also consistent with kleptoplasty, which is the simplest hypothesis to explain photosynthetic activity in *Semitextularia*.

5 Conclusions

Summarizing, *Semitextularia*, an extinct and pioneering multi-chambered calcareous foraminiferal genus (Eifelian, Middle Devonian), shows morphological homology and comparable habitat with the recent photosymbiont-bearing *Peneroplis*. The $\delta^{13}C$ enrichment, up to 2.86‰ in relation to rock matrix samples, indicates that *Semitextularia* could have been kleptoplastic, acquiring and maintaining plastids from their microalgal prey benefit directly from photosynthesis. Another possibility is that these foraminifers maintained algal endosymbionts, which would have involved co-evolution with a microalgal taxon. This beneficial ecological behavior could have had an impact on the evolutionary radiation of calcareous multi-chambered Foraminifera during the mid-Devonian radiation of carbonate-producing biotas.

Author Contributions

ZD developed the original idea presented in the manuscript. ZD and WK designed research. MG performed foraminiferal extraction and prepared samples for isotopic studies. ZD, MG and WK carried out fieldwork. ZD, MG, WK and JH prepared figures. All authors analyzed data and wrote the paper.

Competing Interest Statement

The authors declare no competing interests.

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Figure captions

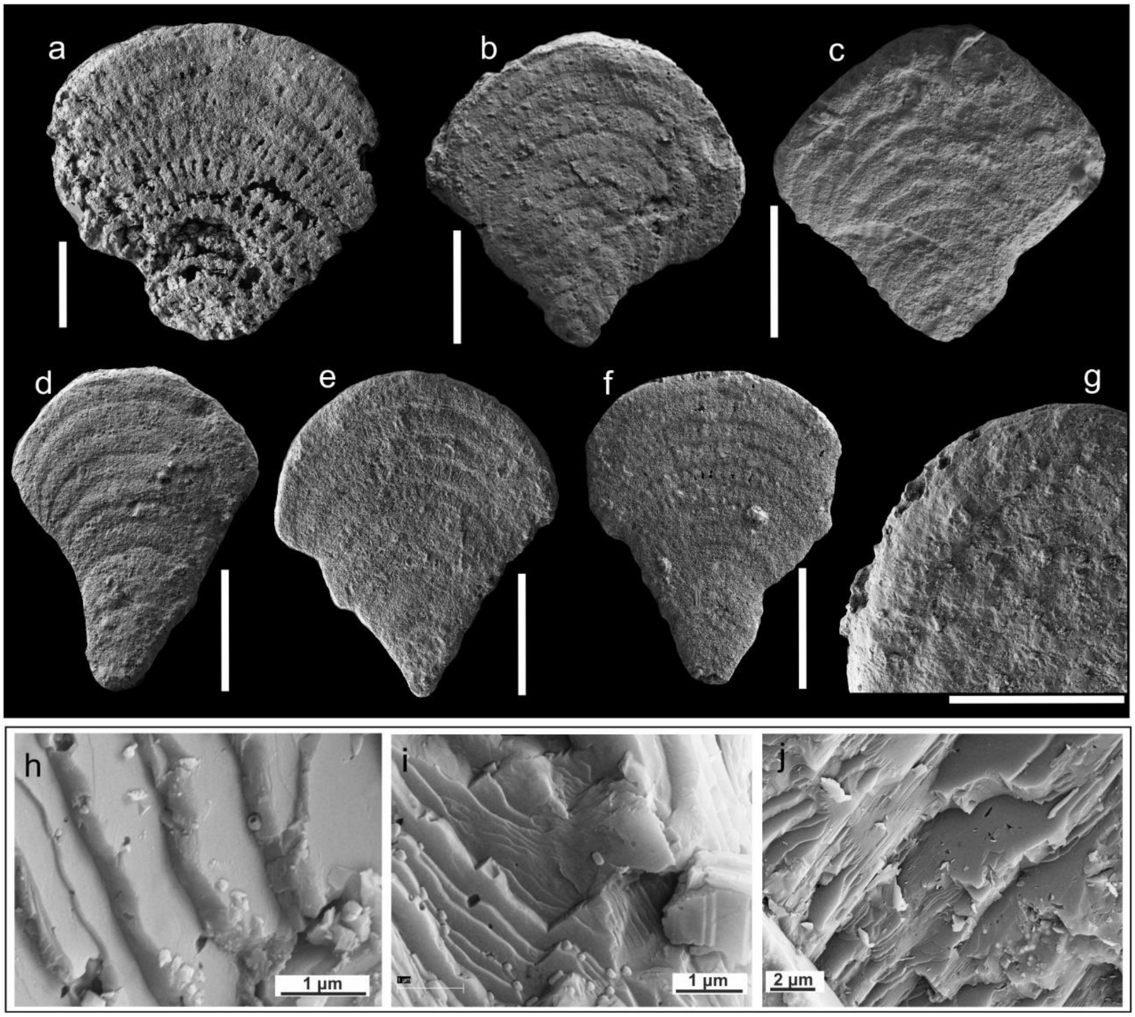

Figure 1. SEM images of *Semitextularia* (Miller and Carmer, 1933) specimens (a–g; scale bars are equal to 100 µm) and cross sections of the *Semitextularia* test (h–j) showing internal lamellar test texture. (a) Miłoszów, sample B1, MWGUW ZI/67/MG7.02. **(b)** Miłoszów, sample 11, MWGUW ZI/67/MG5.03. **(c)** Miłoszów, sample 11, MWGUW ZI/67/MG5.04. **(d)** Miłoszów, sample 12, MWGUW ZI/67/MG5.30. **(e)** Miłoszów, sample 12, MWGUW ZI/67/MG5.27. **(f)** Miłoszów, sample MO, MWGUW ZI/67/MG5.40. **(g)** Miłoszów, sample 12R, MWGUW ZI/67/MG9.23.

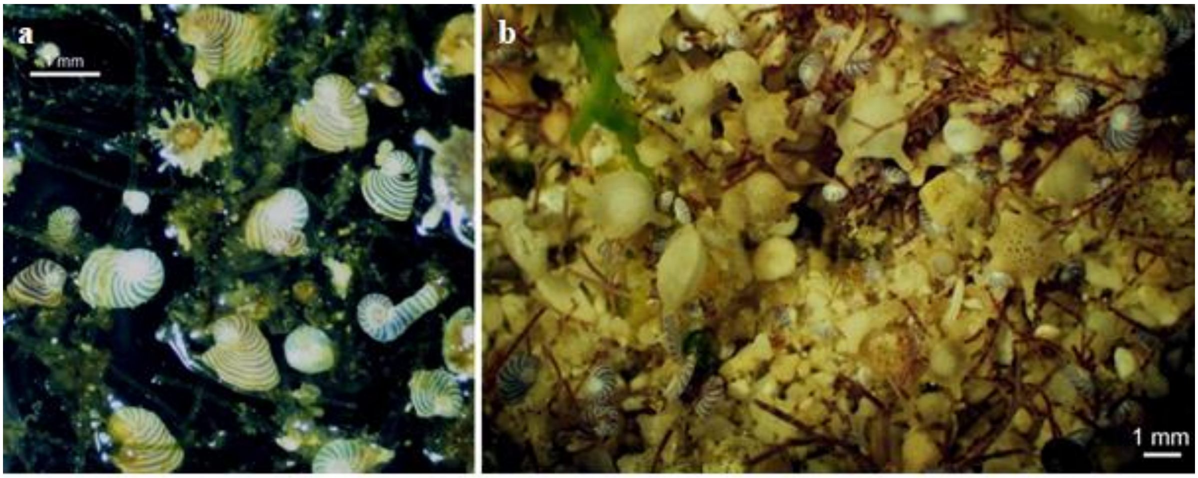

Figure 2. (a) Living peneroplids and *Neorotalia calcar* from algal mats on reef crests in Belau. **(b)** *Peneroplis planatus* attached to filamentous microalgae within sand grains from the reef crest at Sesoko Jima, Japan, together with *Calcarina gaudichaudii* and *Baculogypsina sphaerulata*.

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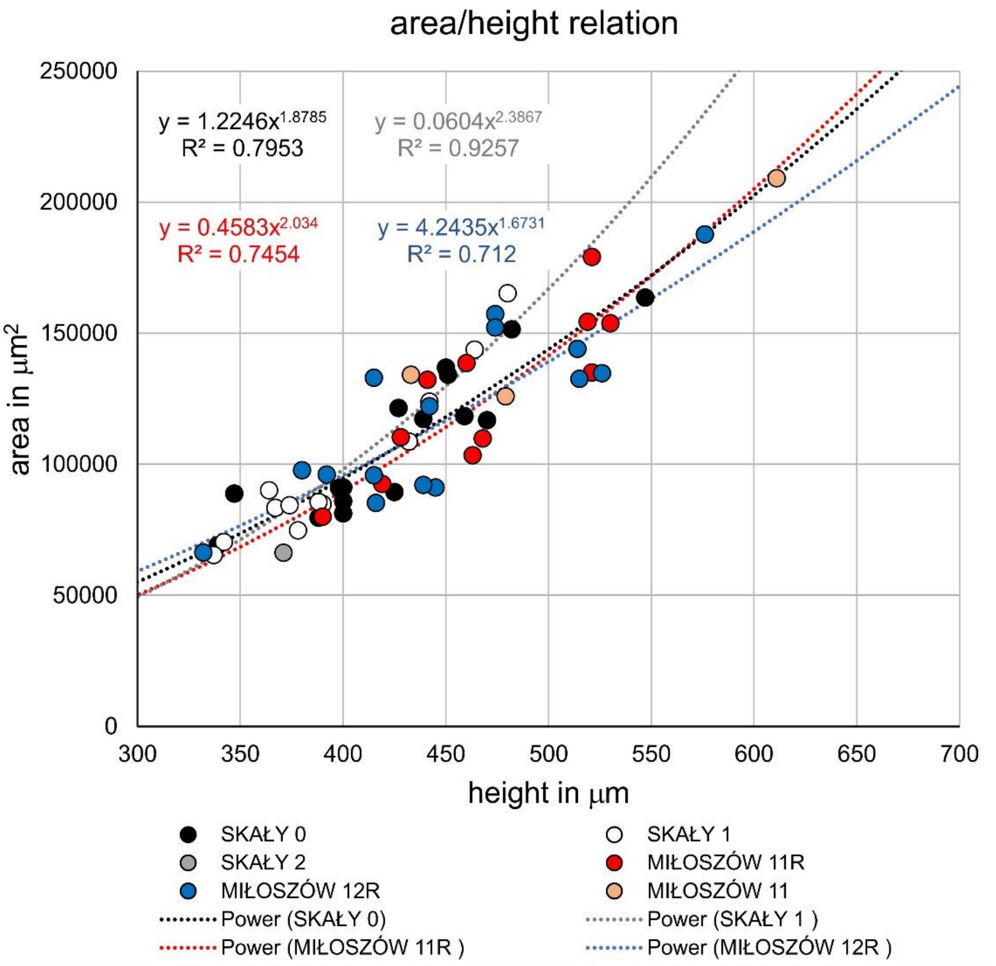

Figure 3. Relationships between test area and test height fitted by power functions.

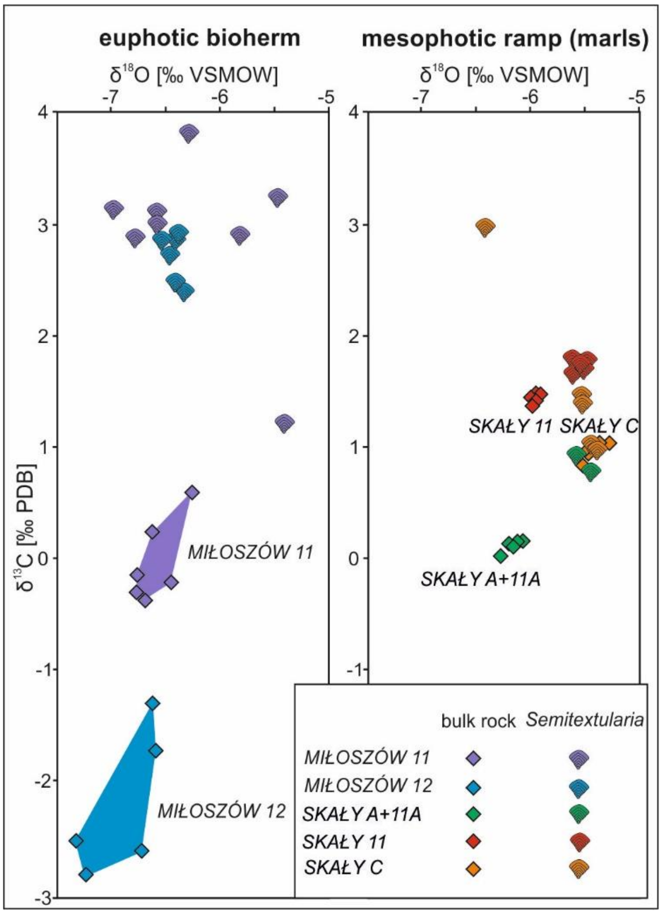

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Figure 4. Variations in δ^{13}C and δ^{18}O values of *Semitextularia* tests and bulk-rock samples from Miłoszów and Skały.

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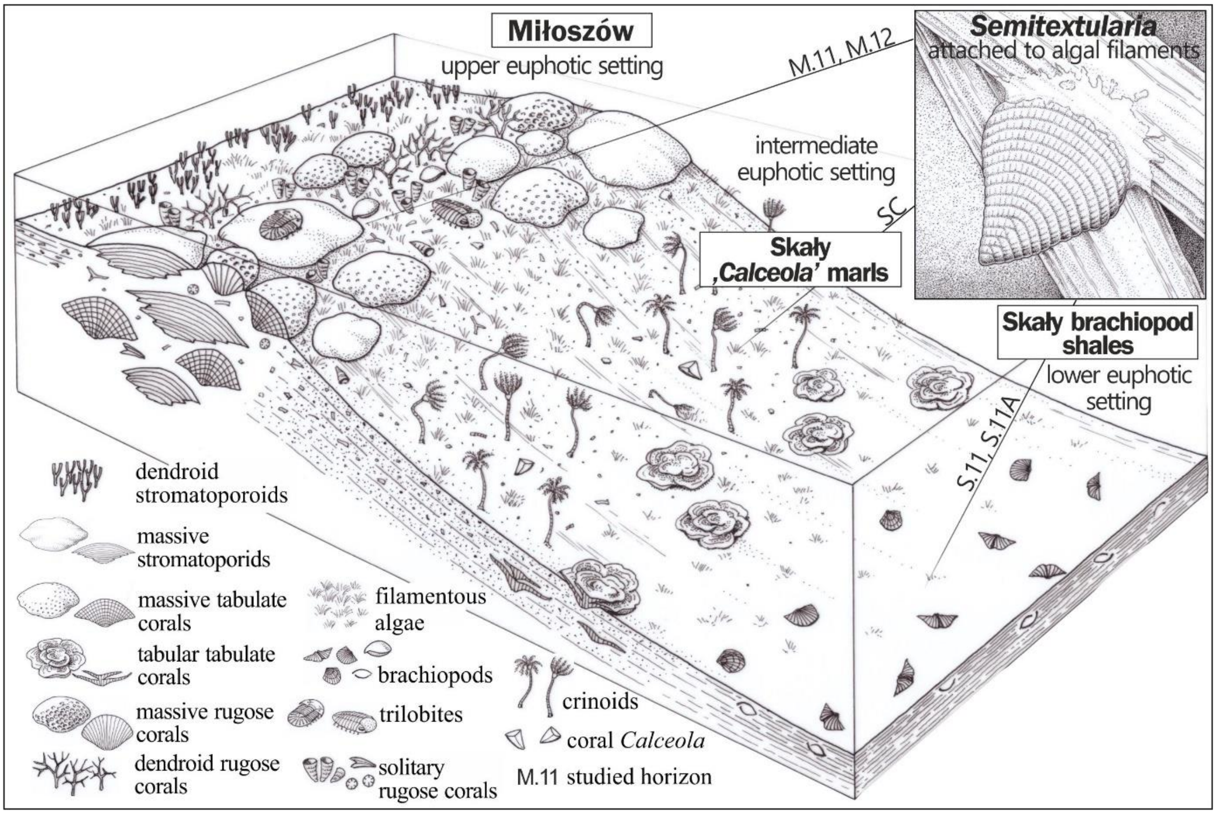

Figure 5. Simplified depositional-biofacies model for the uppermost Eifelian Skały Formation in the Łysogóry basin (HCM), with *Semitextularia*-bearing samples localization.

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