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## Application of biometrical analyses in the determination of the coralline algal genus *Sporolithon* – examples from the Eocene deposits of Omiš (SE Croatia)

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### Abstract

Middle Eocene "Nummulitic limestones" in the area of Omiš (Central Dalmatia), besides the large benthic foraminifera, comprise a rather variable and complex association of bioconstructors, including the warm-water non-geniculate coralline alga *Sporolithon*. We visually distinguished two main types of *Sporolithon* thalii. This study aims to determine *Sporolithon* to the species level and to compare the results with biometrical studies of the size and form of sporangial compartments (diameter- $d$ , height- $h$ , and their ratio- $d/h$ ). We found one taxon similar to the Middle-Upper Eocene Tethyan species *S. lugeonii* (Pfender) Ghosh and Maithy, 1996, considering the shape and number of sporangial compartments, although having some differences in size. Another species, *Sporolithon* sp., has wider compartments, arranged in smaller numbers. The collected specimens of the second species had too few visible compartments for a reliable biostatistical analysis. Biometrical characteristics of reproductive structures of the previously known Eocene *Sporolithon* species helped narrow the choice of similar taxa but were not characteristic enough to determine the species.

**Keywords:** Rhodophyta, *Sporolithon*, biometry, sporangial compartments, Dalmatia

### 1. Introduction

Coralline red algae (Rhodophyta: Corallinophycidae) are generally known for depositing calcium carbonate polymorphs on their cell walls (calcite, dolomite, magnesite, aragonite, low-magnesium calcite), which makes them highly suitable for preservation in the fossil record. They can be divided into 2 morpho-functional groups: geniculate (G) (with non-calcified joints linking calcified segments) and non-geniculate (NG) corallines (lacking such articulations) (Basso, 2012). The group of non-geniculate corallines, with orders Corallinales, Hapalidiales, and Sporolithales is particularly complex in morphological features and therefore complicated for taxonomic studies. Their identification to species level requires the analysis of their reproductive structures (conceptacles or calcified compartments) from the tetra/bisporophytic phases combined with the study of their vegetative characteristics (e.g. the shape of epithelial cells, type of cell connections) (Leão et al., 2020 and references therein). Biometrical methods (e.g. measuring the diameter  $d$  and height  $h$  of compartments and counting their number in a tetrasporangium) are useful in the studies of reproductive structures.

Red algae described in this study occur within olistolites of the Middle Eocene "Nummulitic limestones" (or "Nummulitic breccias") dispersed along the beaches in the Omiš area (Central Dalmatia, SE Croatia), which mark the collapse of the platform edge during the Eocene in the wider region (Sremac et al., 2020, 2024 and references therein). This study aimed to cross-check the taxonomical determinations based on visual characteristics with biometrical studies.



Furthermore, a comparison with other *Sporolithales* taxa from the wider region was presented, in order to evaluate the importance of biometrical studies for the Eocene genera.

## 2. Methods

The study of red algae, whether existing or fossil, includes the field collecting of algal samples and the preparation of thin sections. It is easier to perform such a study on the biological material, while in sedimentary rocks, it is important to prepare a well-oriented cross-section, to get realistic measures, e.g. of the compartment diameter and height.

### 2.1. Field collecting and preparing the *Sporolithon* samples

*Sporolithon* samples (**Figure 1 A-D**) were collected in the area between Omiš and Vruja, at the Stanići beach, with the coordinates: Latitude 43.4152 N, Longitude 16.7239 E. Thin sections from rhodolith samples were prepared at the Department of Geology, Faculty of Science in Zagreb. Cross sections were studied and photographed using the Olympus–SZX10 stereo-microscope. Four samples with *Sporolithon* bioconstructions were recognized, three of them with longitudinally cut sporangial compartments, suitable for measuring.

### 2.2. Biometrical methods

Measurements of compartments were performed by the program Quick Photo Camera connected with the Olympus–SZX10 stereo-microscope, and double-checked by measuring the diameter and height on the printed photomicrographs. The choice of the comparative *Sporolithon* taxa depended on the availability of the compartment size values. The measured dimensions (**Figure 1 D**) are:

$d$  – compartment diameter

$h$  – compartment height

*No.comp.* - number of compartments *per* tetrasporangium.

Results obtained by biometrical methods, including the calculated diameter/height ratio, were compared with the classic paleontological determinations and presented graphically.

## 3. Results

*Sporolithon* samples were analysed using the available palaeontological literature, highlighting the Tethyan region. Representatives of this genus were sometimes originally described under the generic name *Archaeolithothamnium* (e.g. **Studencki, 1988; Moussavian and Kuss, 1990; Aguirre and Braga, 1998; Braga and Bassi, 2007; Bassi et al., 2007** and references therein).

*Sporolithon* bioconstructions occur in two main forms: producing regularly shaped, monospecific, or not very complex rhodoliths (**Figure 1 A**), or, less commonly, irregularly shaped macroids, in combination with acervulinid foraminifera and other red algae (**Figure 1 B**) (**Sremac et al., 2024**). Calcified compartment shapes and their number are also different in these two main types of bioconstructions.

Phylum Rhodophyta Wettstein, 1901

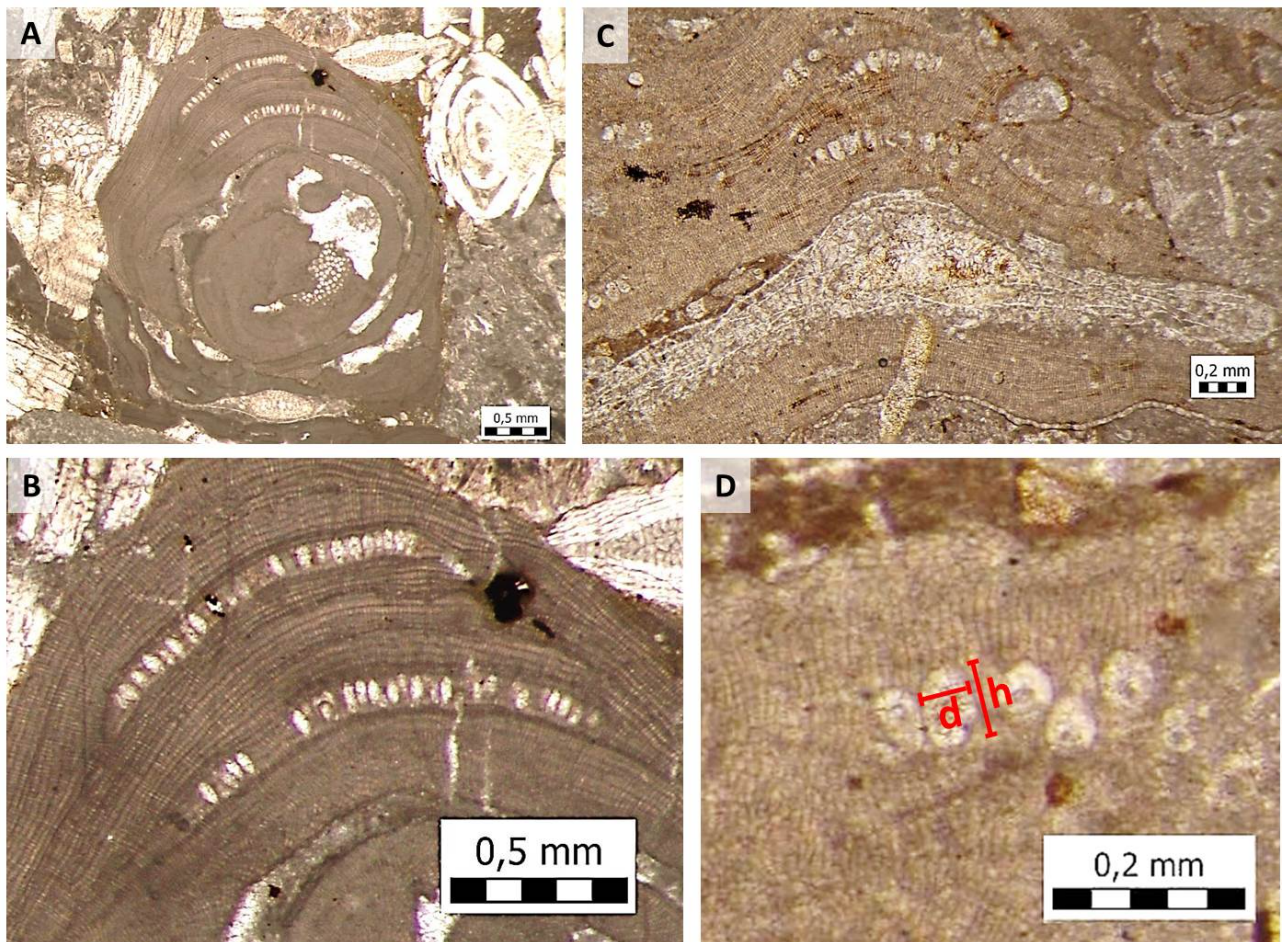
Class Florideophyceae Cronquist, 1960

Subclass Corallinophycidae Le Gall and Saunders, 2007  
Order Sporolithales Le Gall, Payri, Bittner and Saunders, 2010  
Family Sporolithaceae Verheij, 1993  
Genus *Sporolithon* Heydrich, 1897

*Sporolithon lugeonii* (Pfender) Ghosh and Maithy, 1996  
**Figures 1 A, B**

- 1926 *Archaeolithothamnium Lugeoni* - Pfender, p. 324, pls. 9, 12.
- 1996 *Sporolithon lugeonii* – Ghosh and Maithy, p. 68, pl. 1, figs. 1-4.
- 2011 *Sporolithon lugeonii* - Aguirre et al., p. 274-276.
- 2022 *Sporolithon lugeonii* - Aguirre et al., fig. 9 D.
- 2022 *Sporolithon lugeonii* – Hrabovský and Starek, fig. 2.

Two thin sections comprise ca. 4-5 mm wide spherical rhodoliths. One sample comprises only transversal sections, while the other is suitable for measuring the compartment height (**Table 1**). Sporangial compartments, 25 in a row, range from 30-50  $\mu\text{m}$  in diameter, and 60-80  $\mu\text{m}$  in height, the average values are 39.7  $\mu\text{m}$  in diameter and 76.8  $\mu\text{m}$  in height. Specimens from Omiš have a d/h ratio ranging from 0.38-0.71, the average value is 0.52.



**Figure 1:** Cross sections of the genus *Sporolithon* from the Eocene deposits of Omiš, collected during the study Sremac et al. (2020, 2024): A) *Sporolithon lugeonii* rhodolith within the

“Nummulitic limestone”, measured sample 1; B) a detail of the *Sporolithon lugeonii*, Sample 1, with sporangial compartments; C) a crustose *Sporolithon* sp. form overgrowing the foraminifera *Acervulina linearis* and red alga *Lithoporella*, sample 2; D) a crustose *Sporolithon* sp., sample 3, with the position of the measured dimensions:  $d$  = compartment diameter;  $h$  = compartment height.

The species was previously known from the Middle and Upper Eocene deposits of Spain (Pfender, 1926; Aguirre et al., 2011, 2022), the Cretaceous and the Paleogene of India (Rao and Pia 1936; Chaurpagar et al., 2010), and from the Slovak Carpathians (Hrabovský and Starek, 2022) (Figure 2).

The shape of compartments, elongated in the longitudinal section (Figures 1 A, B) and round in oblique-transverse sections (central part of the rhodolith in Figure 1 A) also correspond to the description of *S. lugeonii* offered by Aguirre et al. (2011, 2012).

*Sporolithon* sp. indet.

**Figures 1, C, D**

Two *Sporolithon* specimens have less elongated, oval-shaped compartments, with a smaller number in a sporangium (6 in one specimen and 12-13 in another specimen) in a tetrasporangium (Table 1). They occur in complex bioconstructions, composed of several taxa of red algae, together with acervulinid foraminifera.

The specimen with 10-13 sporangial compartments (Figure 1 C) shows some similarities in compartment shape with the Pacific species *S. kobamazimense* (Ishijima, 1942) from the Eocene of SW Japan (Iryu et al., 2009).

**Table 1:** The dimensions, diameter/height ratio and number of sporangial compartments in three *Sporolithon* bioconstructions from Omiš (**Figure 1**)

Sample/Photo No.	Compartment No.	Compartment diameter d (µm)	Compartment height h (µm)	d/h	No. comp. per tetraspor.
1 /P00033 (Figure 1 A, B) <i>Sporolithon lugeonii</i>	1a1	50	80	0.63	25
	1a2	50	70	0.71	
	1a3	50	80	0.63	
	1a4	30	80	0.38	
	1a5	50	80	0.63	
	1a6	40	80	0.5	
	1a7	40	80	0.5	
	1a8	30	70	0.43	
	1a9	40	70	0.57	
	1a10	40	80	0.5	
	1a11	40	80	0.5	
	1a12	40	70	0.57	
	1a13	30	80	0.38	
	1a14	30	80	0.38	
	1a15	40	80	0.5	
	1b1	50	80	0.63	
	1b2	40	80	0.5	
	1b3	40	80	0.5	
	1b4	40	80	0.67	
	1b5	40	80	0.5	
	1b6	40	80	0.5	
	1b7	40	80	0.5	
	1b8	40	80	0.67	
	1b9	40	80	0.5	
	1b10	40	80	0.5	
	1b11	30	80	0.38	
	1b12	40	80	0.5	
	1b13	40	80	0.5	
	1b14	40	80	0.5	
	1b15	30	80	0.43	
2 /P00121 (Figure 1 C) <i>Sporolithon</i> sp.	2a	50	90	0.56	10-13
	2b	50	90	0.56	
	2c	50	90	0.56	
	2d	50	90	0.56	
	2e	50	90	0.56	
	2f	50	90	0.56	
	2g	50	80	0.63	
	2h	50	80	0.63	
3/P00093 (Figure 1 D) <i>Sporolithon</i> sp.	3a	50	60	0.83	>6
	3b	60	60	1	
	3c	60	90	0.67	
	3d	50	80	0.63	

The specimen presented in **Figure 1 D** slightly resembles the *S. afonense* species (Maslov, 1956) from the Early Eocene of Abhasia (**Bassi et al., 2007**). The number of sporangial compartments available for measuring is too small for a reliable biostatistical study. While the genus *Sporolithon* is rather widespread, the occurrences of *Sporolithon lugeonii* were up to now known from four localities in the Tethyan realm (**Figure 2**).



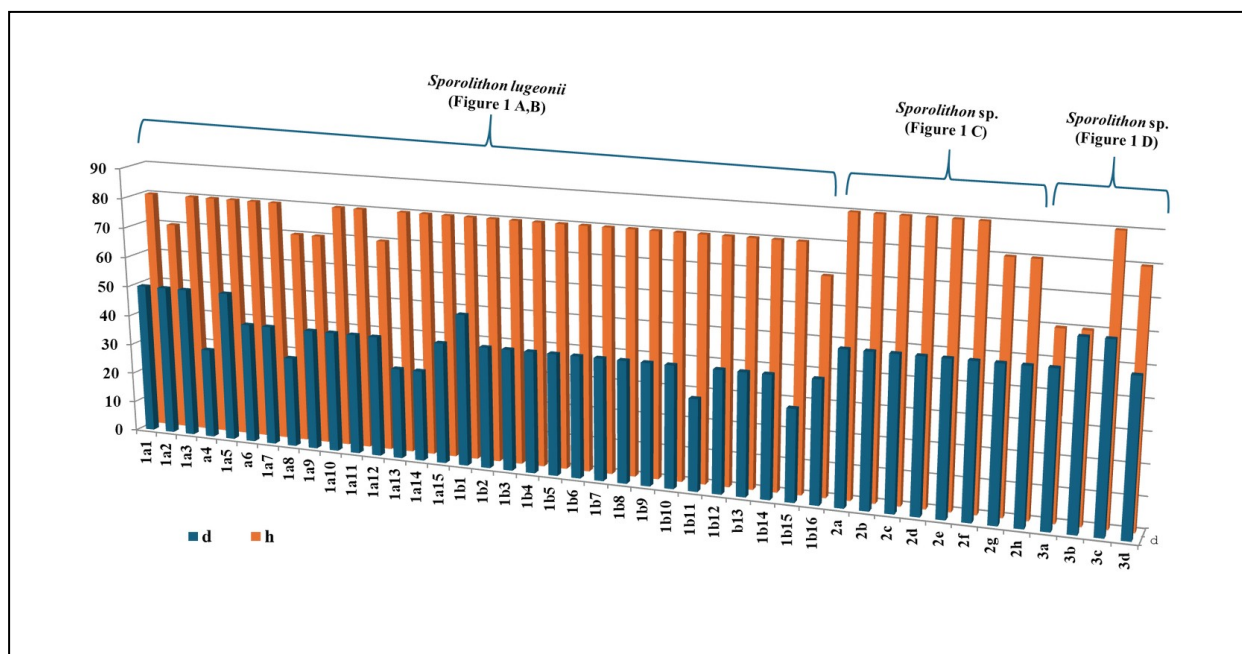
**Figure 2:** Findings of the species *Sporolithon lugeonii* (red circles) on the palaeogeographic map (after Sremac et al., 2024), according to the available literature (Pfender, 1926; Aguirre et al., 2011, 2022; Rao and Pia 1936; Chaurpagar et al., 2010; Misra et al., 2011; Hrabovský and Starek, 2022). The location of Omiš (Croatia) is marked with an asterisk.

#### 4. Discussion

The micropalaeontological study revealed that the four studied samples of *Sporolithon* from the Eocene “Nummulitic limestones” of the Omiš area belong to two (maybe even three) species (Figures 1 A-D, 3; Table 1).

The number of sporangial compartments and their size and shape are different for all three measured specimens (Table 1). The species *Sporolithon lugeonii* (Figures 1 A, B) built irregularly spherical rhodoliths, having up to 25 regularly distributed, elongated calcified compartments.





**Figure 3:** The compartment diameter (d) and height (h) values measured for the three *Sporolithon* samples (Table 1). Specimen 1 (Figure 1 A, B), determined as *Sporolithon lugeonii*, has rather uniformly large sporangial compartments. The differences between the second and third measured specimen (Figures 1 C and D) may be the consequence of the position of the cross sections.

Another two specimens (Figures 1 C, D), determined to the generic level, are characterized by a smaller number of compartments *per* tetrasporangium, the shape of the compartments is less elongated. They compose encrusting forms in combination with *Lithoporella* and acervulinid foraminifera. The d/h ratio is highly variable, even in the same cross-section, which points to unequal positions of the compartment axes. It is also possible that specimens 2 and 3 belong to two different species, but for a more detailed taxonomical study, it would be necessary to have more available fertile *Sporolithon* samples.

The comparison with the *Sporolithon* taxa from the wider region included the study of their sporangial compartments and their shape, in order to confirm the visually done determinations (Table 2, Figures 4 and 5).

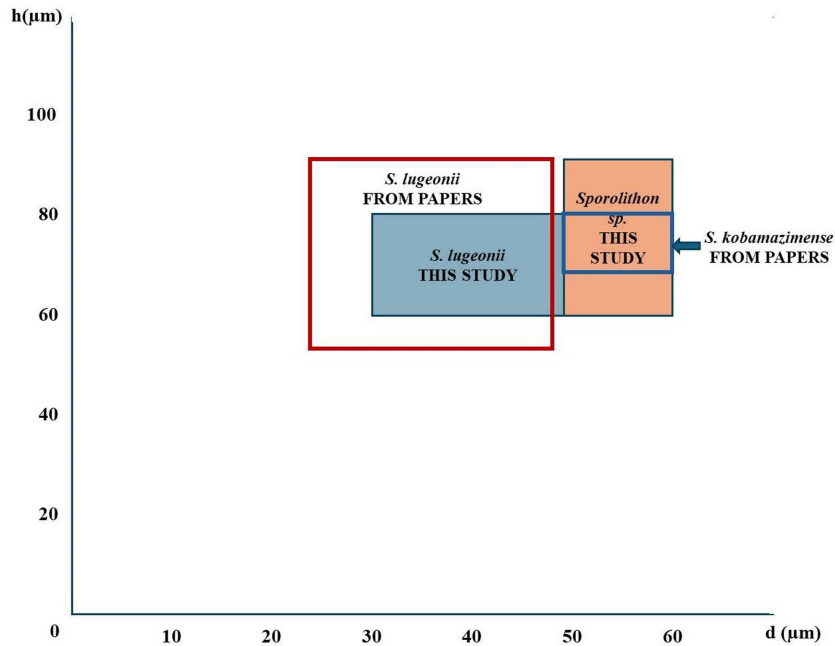
The measurements of the compartment diameters and heights of the Eocene species (Table 2) show a variety of values, sometimes with no clear differences between the taxa.

Comparing the d/h ratio itself also did not contribute enough to the species determination. Specimens 1 and 2 from Omiš have a similar pattern of d/h values, but their sporangial compartments are morphologically clearly different. The variation of d/h values within the sporangial compartments of a single specimen (Figure 3, specimen 3) may be the consequence of the variable position of the compartment axes and therefore is not significant enough for the species determination.

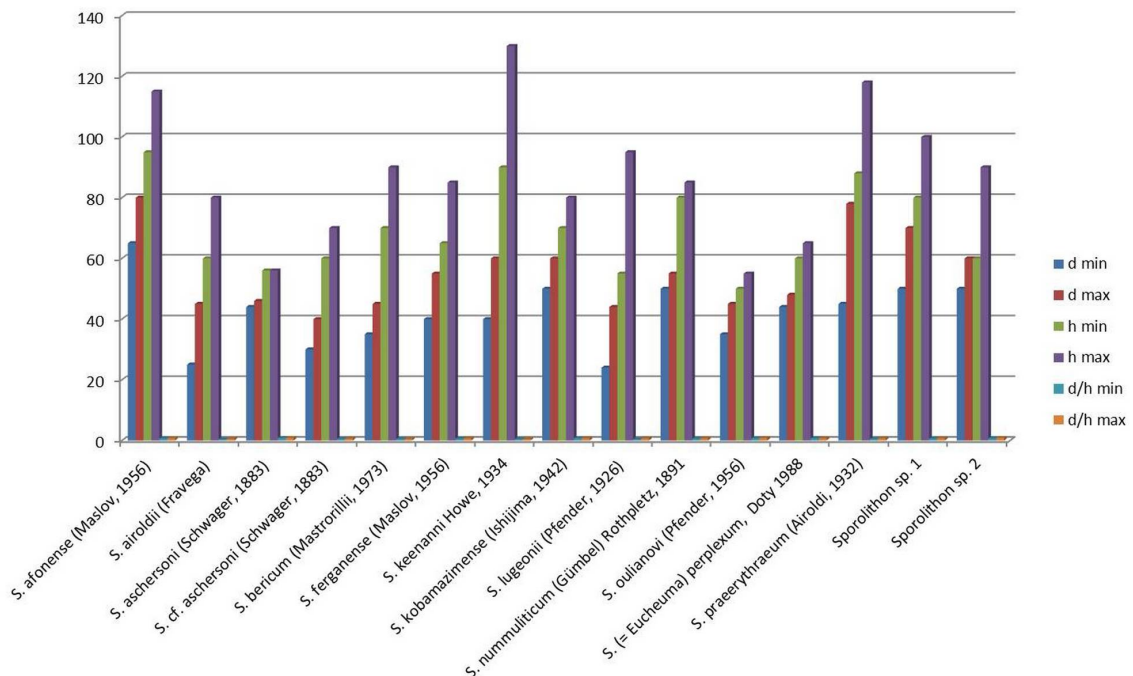
**Table 2.** The list of *Sporolithon* species from the wider region (Verheij, 1993; Townsed et al., 1995; Ghosh and Maithy, 1996; Bassi, 1998; Vannucci et al., 2000; Misra et al., 2011; Chaurpagar et al., 2010; Aguirre et al., 2011, 2022; Basso et al., 2019; Hrabovský and Starek, 2022) with the dimensions of the sporangial compartments.

<i>Sporolithon</i> species		Dimensions (µm) and d/h ratio					
		d min	d max	h min	h max	d/h min	d/h max
From published papers	<i>S. afonense</i> (Maslov, 1956)	65	80	95	115	0.68	0.7
	<i>S. airoidii</i> (Fravega, 1984) Quaranta & Basso, 2010	25	45	60	80	0.42	0.56
	<i>S. aschersoni</i> (Schwager, 1883)	44	46	56	56	0.79	0.82
	<i>S. cf. aschersoni</i> (Schwager, 1883) 1883)	30	40	60	70	0.5	0.57
	<i>S. bericum</i> (Mastrorilli, 1973)	35	45	70	90	0.5	0.5
	<i>S. ferganense</i> (Maslov, 1956)	40	55	65	85	0.62	0.65
	<i>S. keenanni</i> Howe, 1934	40	60	90	130	0.44	0.46
	<i>S. kobamazimense</i> (Ishijima, 1942)	50	60	70	80	0.7	0.75
	<i>S. lugeonii</i> (Pfender, 1926)	24	44	55	95	0.42	0.67
	<i>S. nummuliticum</i> (Gümbel) Rothpletz, 1891	50	55	80	85	0.59	0.69
	<i>S. oulianovi</i> (Pfender, 1956)	35	45	50	55	0.7	0.82
	<i>S. praeerythraeum</i> (Airoidi, 1932)	45	78	88	118	0.5	0.66
	From this study	<b><i>Sporolithon lugeonii</i> (Pfender, 1926)</b>	<b>30</b>	<b>50</b>	<b>60</b>	<b>80</b>	<b>0.5</b>
<b><i>Sporolithon</i> sp.</b>		<b>50</b>	<b>60</b>	<b>60</b>	<b>90</b>	<b>0.67</b>	<b>0.83</b>

Comparing all measured values (minimal and maximal values of diameter and height, together with the minimal and maximal values of the d/h ratio) (Figure 5) can be useful in combination with previous visual determinations. These values point to some similarities among the species, *S. lugeonii* (Figure 4), *S. afonense*, *S. keenanni*, and *S. praeerythraeum* (Figure 5). Biometrical data could be reliably applied to the specimen determined visually as *S. lugeonii*, due to the sufficient number of measurable compartments. The number of compartments for the other two specimens is too small for more precise determinations, and they are determined only at the generic level.



**Figure 4:** The comparison of diameter (d) and height (h) values measured for sporangial compartments of three *Sporolothon* samples (Table 1): The specimen determined as *Sporolothon lugeonii* (Figure 1 A, B) fits well within the biometrical borders of this species. Another two specimens, visually resembling the Pacific species *S. kobamazimense*, have a wider range of compartment heights, but have similarities with this species in compartment diameter and shape.



**Figure 5:** The distribution of maximal and minimal values of the diameter and height, and the diameter/height ratio for the Eocene *Sporolothon* species available in the published papers. *Sporolothon* sp.1 (= *Sporolothon lugeonii*) and *Sporolothon* sp. 2 are the two species from Omiš.



## 5. Conclusions

- The Genus *Sporolithon* (Rhodophyta: Sporolithales) is one of the bioconstructors found in the Eocene "Nummulitic limestones" in Omiš vicinity.
- Fertile specimens have sporangial compartments of different shapes and sizes, pointing to the existence of two (maybe even three) species.
- Some specimens of *Sporolithon* have up to 25 narrow sporangial compartments, ranging in diameter from 30 to 50  $\mu\text{m}$ , and with a height of 60 to 80  $\mu\text{m}$ . They are determined as the species *S. lugeonii*, which has previously been found in the Middle-Upper Eocene deposits.
- The two specimens determined as *Sporolithon* sp. have less than 13 oval compartments in a cluster, ranging in diameter from 50 to 60  $\mu\text{m}$ , and with a height of 60 to 90  $\mu\text{m}$ . They remain determined at the generic level.
- Measured values can be an additional tool in taxonomical studies of *Sporolithon* species, but only in combination with visual determinations.
- More *Sporolithon* samples should be measured, including the additional study of their fertile and vegetative parts, in order to obtain more precise taxonomical conclusions for the Sporolithales from Omiš.

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## SAŽETAK

## Značenje biometrijskih analiza za taksonomsku odredbu vrsta roda *Sporolithon*: primjeri iz eocenskih naslaga Omiša

U numulitnim vapnencima eocenske starosti na području Omiša nađeni su raznoliki ostatci crvenih algi, među kojima i predstavnici toplovodne skupine Sporolithales. Ove alge imaju složenu građu kalcificiranih segmenata, pa ih je teško determinirati na razini vrste. Fertilni primjerci koje smo pronašli tijekom ovog istraživanja razlikuju se prema izgledu, broju i veličini sporangijskih odjeljaka, pa su radno bili determinirani kao dvije vrste roda *Sporolithon*. Prva vrsta ima niz karakteristika bliskih vrsti *Sporolithon lugeonii* (Pfender, 1926), s kojom dijeli broj odjeljaka u tetrasporangiju. Sama je vrsta varijabilne veličine, no ima uske kopljaste odjeljke, koji su gusto i dosta ravnomjerno raspoređeni. Preostala dva pronađena primjerka determinirana su samo na razini roda (*Sporolithon* sp.), imaju manji broj širih odjeljaka, pa im je omjer dijametra i visine odjeljaka (d/h) veći. Mjerenja odjeljaka dala su dosta varijabilne rezultate, koji otvaraju mogućnost da *Sporolithon* sp. zapravo sadrži dvije različite vrste, no sačuvan je premali broj odjeljaka za validnu biometrijsku analizu. Za detaljnije taksonomsko istraživanje roda *Sporolithon* potrebno je dodatno uzorkovanje, a ova preliminarna studija je pokazala da samo biometrijsko istraživanje nije dostatno, već je potreban kombinirani pristup, koji će uz veličinu uzeti u obzir i njihove druge reproduktivne i vegetativne karakteristike.

**Ključne riječi:** Rhodophyta, *Sporolithon*, biometrija, sporangijski odjeljci, Dalmacija

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### Author’s contribution

**Jasenska Sremac (1)** (retired full professor, paleontologist) provided the fieldwork, micropalaeontological analyses, interpretations, and presentation of the results. **Filip Huić (2)** (anthropologist and linguist, highly involved in palaeontology) provided the fieldwork, measurements, and the database of contemporary taxa. **Marija Bošnjak (3)** (senior curator, palaeontologist) provided the biostatistical analyses and associated interpretations.