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Zeapora PENECKE 1894 redefined: a halimedacean alga

BERNHARD HUBMANN¹

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Revision von Zeapora PENECKE 1894: eine halimedale Grünalge

Zusammenfassung

Zeapora PENECKE 1894 galt in der Literatur bislang als eines der ältesten Dasycladales-Taxa. Wie Untersuchungen des Lectotypus unter Einbindung von neu aufgesammeltem Material an der Typuslokalität zeigen, muß mit Entschiedenheit Zeapora von den Dasycladales verwiesen werden. Eine Zuordnung zu den Halimedaceen wird vorgenommen.

Abstract

The Middle Devonian Zeapora PENECKE 1894 has been interpreted as one of the oldest dasycladalean alga. Re-study of the lectotype and investigation of new collected material at the type locality suggest a taxonomic shift of Zeapora to the halimedacean green algae.

1. Geological frame

The highly fossiliferous Middle Devonian (Eifelian) sequence, the "Barrandei-Limestones" (called after the heliolitid tabulate coral *Pachycanalicula barrandei* (PENECKE 1887)), of the Graz Palaeozoic (Southeast Austria) has been a prominent study topic for palaeontologists since the 1840's. This shallow marine formation, well known for its *Thamnophyllum*fauna, contains rare remains of calcareous green algae (HUB-MANN 1990; 1993).

Findings of Zeapora are restricted to one single outcrop of the entire Graz Palaeozoic. Due to inadequate descriptions (PENECKE 1894, HERITSCH 1915, FLÜGEL 1959) a confusion exists concerning the exact location of Zeapora within an old quarry area some 5 km west of Graz. The newly collected material derives from the eastern part of the closed illite-mine at Steinberg road (Fig. 1) at the southern slope of the Kollerkogel.

2. Zeapora's History

In 1894 Karl Alphons PENECKE published a monograph on the Devonian of the Graz Palaeozoic. In this important publication on its fossil content he described remains "consisting of a hollow central axis surrounded by only one row of prismatic cells". He named the new genus *Zeapora*. The genus was designated by monotypy; its type species *Zeapora gracilis* remained the only known species. PENECKE (1894, p. 610) assigned it to a cyclostomate bryozoan "to which it surely belongs judging from its looks". In 1938 RUKHIN erected the new family Amphiporidae in his "Lower Paleozoic Corals and Stromatoporoides of the upper part of the Kolyma river" (original in Russian). He included in this family *Amphipora, Idiostroma, Haraamphipora*, and also *Zelopora* PENECKE, 1894. In all probability *Zelopora* is a confusion caused by mistake in writing or printing instead of *Zeapora*.

The volume G of the "Treatise on Invertebrate Paleontology" was published in 1953. BASSLER (1953) mentiones Zeapora

Address of the author

¹ Bernhard HUBMANN, Institut für Geologie und Paläontologie, Karl-Franzens-Universität Graz, Heinrichstrasse 26, A-8010 Graz e-mail: bernhard.hubmann@kfunigraz.ac.at



Fig. 1

Location of the Zeapora gracilis PENECKE, 1894.

Note: buildings in the right half of the figure belong to the urban district of Graz (Wetzelsdorf). **1** indicates the famous restaurant "Zum Feliferhof" (now a China inn) which has been often cited in the old literature. **2** a little chapel at the road fork to the abandoned quarries at the southern slope of the Kollerkogel. **3** quarry-area within the "Barrandei-Limestones" containing *Zeapora* (eastern part of the quarry; arrow). Up to 1952 illite was exploited at the western sector.

without further remarks as a representative of Trepostomates (Part G:236) in a list of "Unrecognized generic names applied to Bryozoans". In his publication about "Tabulates of the Palaeozoic of the European Part of the SSSR" (original in Russian) SOKOLOV (1955) assigned Zeapora with some restrictions to thamnoporid tabulate corals. H. W. FLÜGEL (1959) was the first to recognize the algal nature of Zeapora when studying material collected and taxonomically determined as Zeapora gracilis. However, FLÜGEL essentially followed PE-NECKE's original description of a "hollow central axis". He interpreted it as a "hollow, single 'Stammzelle' [= central cylinder] round in diameter" from a dasycladacean algae. ENDO (1961, p. 6) published the same interpretation and pointed out "somewhat intimate relationships with genus Koni[n]ckpora in having cylindrical thalli with evenly radiated branches which are strongly encrusted with calcium carbonate". RIDING (1979, p. 141) mentioned Zeapora as a codiacean alga without any further comment on its systematic position.

3. Material

Karl Alphons PENECKE worked without any remuneration for 22 years at the Graz Institute, until a professorship at Chernovtsy University (now: Ukraina) was offered to him. He transferred with him his 'private' collection (including type material) (MEIXNER, 1958). Unfortunately Chernovtsy was seriously damaged in World War I and PENECKE's material is lost.

Fortunately, in the type collection of the Graz University samples are stored containing Zeapora. One of them, determined as *Striatopora* aff. *subaequalis* (a tabulate coral!) was collected in 1888. The other sample was aquired in 1894, the year of Zeapora's publication. The latter sample was PE-NECKE's gift to the University collection as one can see on the label (Fig. 2). There are also two thin sections from this sam-



Fig. 2

Label of a sample of *Zeapora gracilis* from the type locality ("Kollerko-gel") with the remark "Penecke don[at]."

ple which were choosen as lectotype of *Zeapora* by FLÜGEL (1959). Preservation is not good and curtails the taxonomic recognition of critical structures. Recently collected material at the type locality has a better state of preservation calling for a taxonomic emendation and systematic redefinition.

4. Phytography

Original description of the genus (according to PENECKE 1894):

Stock rasenförmig. Die Aeste bestehen ausser einer centralen hohlen Achse, um die die kurzen prismatischen Zellen in dicht gedrängten Spiralen wie die Körner an einem Maiskolben in einer peripheren Schichte sich anreihen. In der Tiefe sind die Zellen dünnwandig, polygonal, ziemlich regelmässig sechsseitig, gegen die Mündung hin sehr dickwandig, die terminale Mündung selbst kreisrund, das Lumen hat dadurch die Gestalt eines kurzhalsigen Kolbenfläschchens mit sechsseitiger Basis.

Translation:

Colony meadow-like. Branches consist of hollow axes with short prismatic cells pressed closely together in spirals like grains of a corn-cob; they are arranged in a peripheral layer. In the deep [proximal] cells are thin-walled, polygonal, regularly hexagonal and very thick-walled against their terminations. Peripheral part of the termination circular, shape of lumen thereby like a short-necked flask with a hexagonal bottom.

Original description of the type species Zeapora gracilis (according to PENECKE 1894):

Die zarten Aestchen besitzen einen Durchmesser von 1 bis 1.8 Millimeter. Der Querschnitt der centralen Hohlachse ist rosettenförmig, 5-6-luppig, sein Durchmesser gleich einem Drittel des Astdurchmessers. Die Höhe einer polygonalen Zelle beträgt circa 0.5 Millimeter, ihr Durchmesser an der Basis circa 0.25 Millimeter, der Durchmesser der Mündung beiläufig die Hälfte davon. Die Abstände der kreisrunden Mündungen auf der Oberfläche der Aestchen sind daher beiläufig gleich ihrem Durchmesser. In den Querschnitt eines Astes kommen 10-15 Zellen zu liegen, deren ideelle Längsachse nicht vollständig senkrecht auf den Centralcanal steht, sondern etwas schräg nach aufwärts gegen das Astende geneigt ist. Verzweigungen konnte ich an den vorliegenden Astfragmenten nicht beobachten.

Translation:

Delicate branches 1 to 1.8 mm in diameter. Cross-section of the central hollow axis rosette-like with 5 to 6 convexities like puddle balls, the diameter approximately one third of the branch diameter. The height [length] of a polygonal cell is approximately 0.5 mm, the diameter at its base approximately 0.25 mm; diameter of the termination about one half of it. Therefore distances of circular terminations on the surface of branches and their diameters are approximately the same. Within a cross-section of a branch 10-15 cells are developed with their ideal longitudinal axes not perfectly vertical to the central channel but slightly oblique upwards and inclined to the end of the branch. Ramifications on studied fragments of branches could not be detected.

The newly collected material of the type location and the (re)study of more than 60 thin sections that contain up to 600 fragments (in one thin section!) of *Zeapora* suggest new taxonomic and systematic interpretations. "White-card-investigation" (FOLK 1987) and darkfield observations of thin-sections clearly exhibit the anatomic features.

(a) Eidonomy

Environmental investigations of algal thalli bearing horizons within the Barrandei-Limestones point to quiet hydrodynamic conditions (HUBMANN 1993, 1997). Patches with high concentrations of *Zeapora* fragments within algal bearing horizons are interpreted as algal meadows with individual plants disar-



Fig. 3

Biometric data of Zeapora gracilis, n ... number of measurements; dimensions in μ

3A ... cross-section within the median plane of cortical filaments showing typically bowl-shaped distal terminations.

3B ... cross-section with round to slightly elongated cortical filaments.

Box-plots with median values (black squares), lower and upper quartiles (terminations of the box) and whiskers (minimum and maximum values)

ticulated in situ. Nevertheless no complete specimen, but only single branches could be found within the black carbonaceous micritic limestones. Fragments of thalli are usually about 5 mm up to 15 mm in length, the common diameter about 1.35 mm (cf. Fig. 3). Fragmented thalli are straight, rarely curved, and tapering to the distal end. The surfaces are covered with close-set dents.

(b) Anatomy

The thalli clearly show numerous peripheral tubules (commonly filled with coarse-grained sparite but also with black to light-grey micrite) arranged around a "circular hollow steam" in the sense of PENECKE. Using the "white-card-method" (FOLK 1987) and illumination by darkfield condensator, contrasts of primary structures are intensified and expose a central axis filled by a bundle of medullar filaments! The medullar zone, usually 390 to 400 μ in diameter, consists of 4 to 6 (up to 10 and more) slightly interwoven filaments. Their diameters vary between 80 to 210 μ . The cortical zone is filled by massive carbonate deposits and perforated by roundly-elongated, densely packed filaments. Cortical filaments vary considerably in longitudinal and cross sections due to different orientation of their bowling-like shapes (Fig. 3A vs. 3B). In some specimens, they seem to be segmented.

5. Systematic shift

The presence of characteristic internal structures, i.e. development of a number of medullar filaments (Fig. 4; Fig 5a-d), excludes Zeapora from the dasycladales. The anatomic arrangement of a well defined medullar and cortical zones together with its characteristically developed filaments identifies Zeapora as a halimedacean green alga. Concerning its rounded big cortical filaments Zeapora shows some similarities with Botrys SCHIRSCHOVA 1985, "Litanaia" grandis PANTIC 1973 and Uva suspecta MASLOV 1956 (see MAMET 1998, p. 23-24 for re-interpretation).

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Fig. 4

Various sections of Zeapora gracilis showing the internal variation. Note the alternation of rounded and bowl-shaped cortical filaments in longitudinal and oblique sections (cf. Fig. 3A vs. 3B) of thalli.



Zeapora PENECKE 1894 redefined: a halimedacean alga



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– Fig.5

Sections of Zeapora gracilis PENECKE, 1894

(a)

Cross-section. Note the rosette-like medullar zone and massive calcareous cortex; magnification: 62x

(b)

Oblique cross-section exhibiting a medullar zone consisting of several central filaments; magnification: $62 x^{\circ}$

(C)

Slightly oblique longitudinal section. Note typically polygonal contours of cortical filaments in marginal sections (upper part of the thallus) and alternation of rounded and bottle-shaped cortical filaments (the latter with their "necks" orientated to the termination of the thallus); magnification: 29x

(d)

Oblique section with sparitic filaments; magnification: 79x