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DEVONIAN UDOTEACEAN GREEN ALGAE FROM THE CANTABRIAN MOUNTAINS (SANTA LUCÍA FORMATION), NW-SPAIN

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ABSTRACT

The erect Udoteacean green algae *Pseudopalaeoporella lummatonensis* (Elliott, 1961) and *"Litanaia" graecensis* Hubmann, 1990 are described from the Santa Lucía Formation (Lower to Middle Devonian; Upper Emsian to Lower Eifelian) at Geras de Gordón (NW-Spain, Cantabrian Mountains). Investigations of the depositional environment of the sections containing udoteacean thalli indicate a position in a protected subtidal area on a gently inclined ramp. Floristic and biogeographical relations are discussed.

Keywords: Calcareous Green Algae (Udoteaceans), Lower Devonian (Emsian), Spain, Systematics, Biogeography.

RESUMEN

Se describen dos especies de algas verdes udoteáceas erectas, *Pseudopalaeoporella lummatonensis* (Elliott, 1961) y *"Litanaia" graecensis* Hubmann, 1990, procedentes de la Formación Santa Lucía (Devónico Inferior a Medio; Emsiense superior a Eifeliense inferior) en la localidad de Geras de Gordón (Cordillera Cantábrica, NW de España). Las investigaciones sobre el medio de depósito indican que su desarrollo tuvo lugar en un área submareal protegida situada sobre una rampa suavemente inclinada. Se señalan las relaciones florísticas y biogeográficas.

Palabras clave: Algas Verdes Calcáreas (Udoteáceas), Devónico Inferior (Emsiense), España, Sistemática, Biogeografía.

ZUSAMMENFASSUNG

Aus der Santa Lucía Formation (Unterdevon bis Mitteldevon; oberes Emsium bis unteres Eifelium) bei Geras de Gordón (NW-Spanien, Kantabrisches Gebirge) werden Vertreter der Udoteaceen beschrieben: *Pseudopalaeoporella lummatonensis* (Elliott, 1961) und *"Litanaia" graecensis* Hubmann, 1990. Fazielle Untersuchungen der Profile lassen als Ablagerungsraum einen geschützten subtidalen Bereich einer schwach geneigten Rampe annehmen. Floristische und biogeographische Überlegungen werden angestellt.

Schlüsselwörter: Kalkgrünalgen (Udoteaceen), Unterdevon (Emsium), Spanien, Systematik, Biogeographie.

LOCATION

The samples containing udoteacean green algae were collected from outcrops near the small village Geras de Gordón (Fig. 1) west of La Pola de Gordón (Bernesga Valley, province León; NW-Spain). The specimens were recognized in patches in black organic-rich limestones (Herrmann, 1990). The thin sections are stored at the Karl-Franzens-University, Graz, Institute of Geology and Palaeontology, under the code-number UGP 3023.

GEOLOGICAL AND STRATIGRAPHICAL FRAMEWORK (R. Herrmann)

The sediments of the Santa Lucia Formation and the Moniello Formation, its Asturian counterpart, have been studied by several authors, e.g., de Coo *et al.* (1971), de Coo (1974), Méndez Bedia (1978), García López (1987), Hermann (1990), Soto *et al.* (1994), Méndez Bedia *et al.* (in press).

The shallow marine limestones of the Santa Lucía Formation (Upper Emsian to Lower Eifelian) were deposited on a gently southward inclined carbonate ramp at the southern margin of an emerged area, the Asturian High. At Geras de Gordón the Santa Lucía limestones contrasts sharply from clays of the underlying La Vid Formation.

The succession begins (Fig. 2) with crinoidal grainstones alternating, with a clayey facies rich in brachiopods, bryozoans, tentaculites, crinoids and trilobites (Brachiopod/Bryozoan facies). Then finer grainstones and packstones with chert (Packstone facies) grade into black coloured biostromal limestones. *Thamnopora* sp. and less frequently Udoteacean meadows are characteristic, as are beds with lamellar and domal shaped tabulate

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corals and stromatoporoids. Some small patch reefs consisting mainly of stromatoporoids also occur (Biostrome/Patchreef facies).

After this middle part of the succession, which is quite resistant to erosion, black biostromal floatstones are followed by packstones (containing chert) and by a thick sequence of crinoidal grainstones (encrinites).

In the upper part biostromes are erected by stromatoporoids, chaetetids and cnidarians. Crinoidal/bryozoan grainstones with intercalations of brown coloured Brachiopod/Bryozoan floatstones terminate the succession.

There is a tendency towards regression in the middle part of the Santa Lucía Formation where short intervals of bahamites with *Amphipora* sp. (Bahamite facies) and cyanophycean bindstones with fenestral fabric (Loferite facies) are observed.

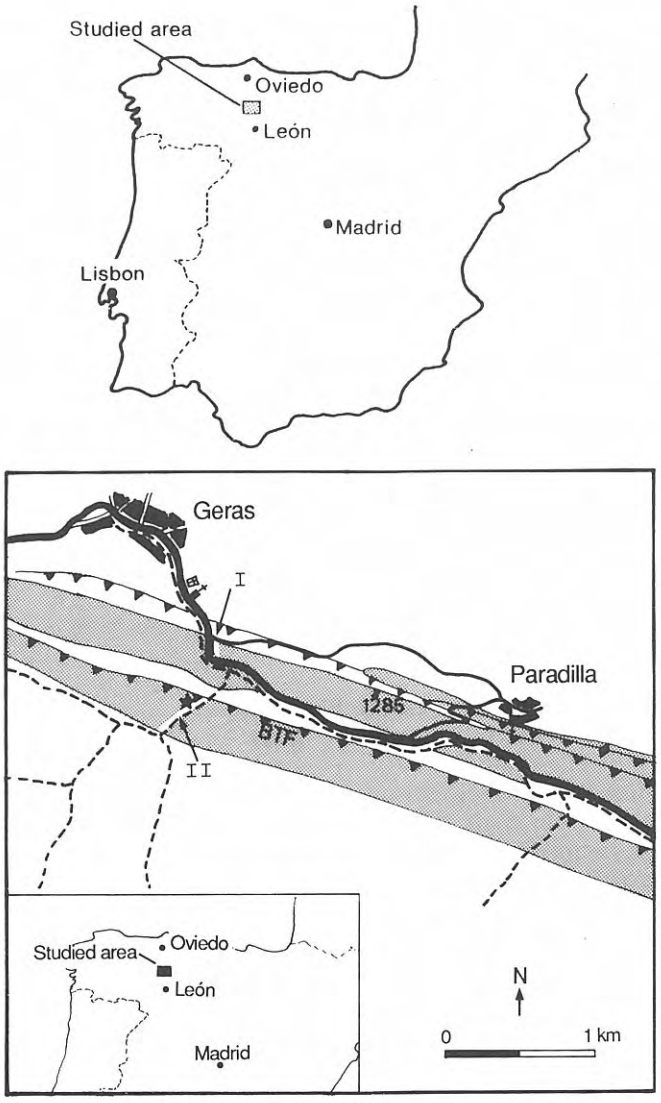


Figure 1. Location of the area studied and the sections I and II shown in Fig. 2 (left and right stratigraphic column). The Santa Lucía Formation (shaded) is partly duplicated by the Beberino thrust fault (BTF), with a narrow strip of Huergas Formation (white) occurring in between. The samples with udoteacean algae (star) were taken from the southern occurrence of the Santa Lucía Formation.

The sequence becomes transgressive in the massive middle part of the section. Eventually, carbonate sedimentation ended with the drowning of the entire carbonate platform. Clayey siltstones with turbidite intercalations of the Huergas Formation (García-Ramos, 1977) overlie a sedimentation hiatus.

Precise biostratigraphy of the Santa Lucía Formation is not clearly identifiable at this stage due to the scarcity of fossils. A few conodonts indicate the Upper Emsian (*serotinus* zone) (Grötsch, 1988), while the upper parts are assumed to be Lower Eifelian (*costatus* zone) (Buggisch *et al.*, 1980, García-López, 1987). In contrast García-Alcalde *et al.* (1979) favours a col/co2 brachiopod boundary at the top of the Santa Lucía Formation. Since the bed which contains the udoteaceans is situated in the lower half of the succession, we assume that the algae are of Early Devonian (latest Emsian) in age.

ENVIRONMENTAL INVESTIGATIONS

The limestones of the Santa Lucía Formation were deposited on a gentle southward inclined ramp, which was subdivided by crinoidal sand bars into a landward protected area (intertidal and protected subtidal) and a seaward open marine area (open subtidal).

Six facies types, which can be subdivided into 15 types of microfacies, are recognized (Herrmann, 1990) (Fig. 3).

Generally, mudstones and cyanophycean bindstones predominate in the intertidal environment. In the protected subtidal facies belt stromatoporoid/cnidarian floatstones, udoteacean float/bafflestones, *Thamnopora* float/bafflestones and bioclastic packstones –all of dark grey to black colour– form over Biostrome-Patchreef facies.

The open marine seaward area of the crinoidal sand bars is represented by yellowish and brown clayey packstones rich in crinoid ossicles, bryozoans, brachiopods, tabulate corals, tentaculites and trilobites.

Interfingerings with adjacent facies help to define the position of the udoteacean meadows in this "facies mosaic" rather precisely. The udoteacean meadows occur near and intersect the following facies types:

– Stromatoporoid/cnidarian facies
– *Thamnopora* facies
– Bahamite facies

The bed rich in udoteaceans is intercalated in strata of stromatoporid/cnidarian facies. The latter is characterized by the abundance of stromatoporoid and chaetetid sponges as well as by tabulate and rugose corals lying in dark bioclastic packstones or wackestones. These biostromes exhibit the highest organism diversity.

Limestones containing thalli of udoteaceans also occur near to the *Thamnopora* facies. Besides *Thamnopora* sp., stromatoporoids, rugose corals and fistuliporid bryozoans are the main constituents. These organisms lie in an often bioturbated matrix of dark-coloured bioclastic packstones. Like the other biostromal facies, the *Thamnopora* meadows grew in a shallow, protected subtidal environment.

The influence of the Bahamite facies and the Grain-

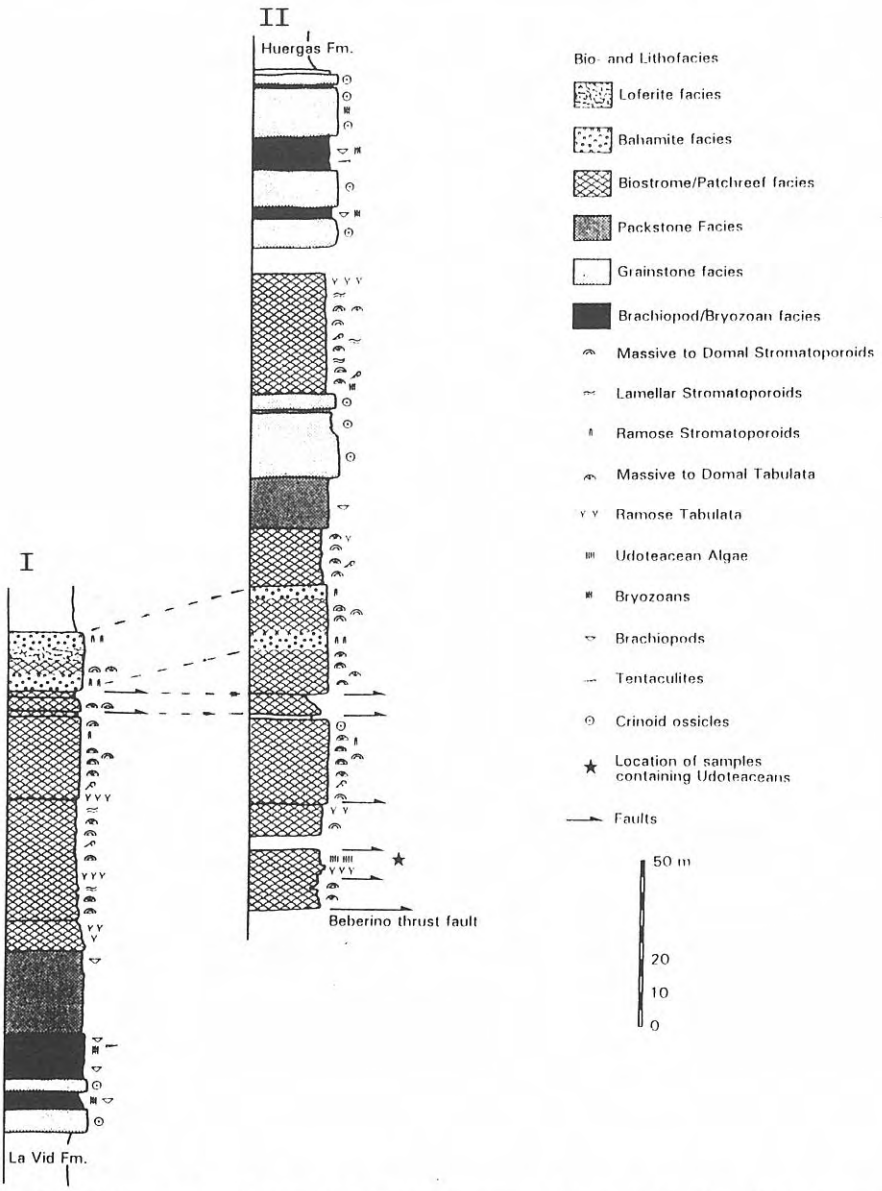


Figure 2. Composite stratigraphic column of the Santa Lucía Formation near Geras de Gordón. The lower part of the section I (left column) was measured along the road Beberino-Geras, beginning at the contact with the La Vid Formation directly south of the path to Paradilla and reaching up to the top of the very massive resistant member of the succession. Due to better exposure, the upper part of the section II (right column) was measured south of the road Beberino-Geras along the western side of the Arroyo de Boyeriza valley. It starts above the Beberino thrust fault and ends with the last limestone beds of the Santa Lucía Formation.

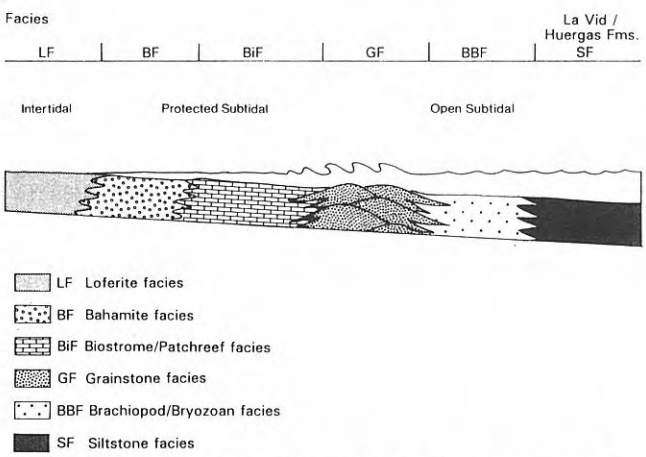


Figure 3. Schematic section through the Santa Lucía carbonate ramp showing the arrangement of the different facies types.

stone facies is shown by the occurence of lumps and grapestones and by crinoidal debris.

Transitions to the stromatoporoid/cnidarian and the *Thamnopora* facies and the influence of the Bahamite facies and grainstone bars on the udoteacean meadows point to a protected subtidal position. Moreover, the dark colour of the limestones, caused by organic matter as well as relatively high amounts of clay, also indicate calm sedimentary conditions.

Comparable distribution patterns of Devonian calcareous green algae are developed in south- and austroalpine units of the Alps (Fenninger & Hubmann, in press).

SYSTEMATIC PALAEONTOLOGY
(B. Hubmann)

In 1893 Stolley described some Ordovician algae in erratic boulders of Sweden. He compared them with the recent Dasycladacean *Bornetella* and assigned them to the genus *Palaeoporella*. Pia (1926: 133, 1927: 59) assigned *Palaeoporella* to the codiaceans, because of the multiple bifurcated filaments. Hurka (1968) supposed that codiacean (udoteacean) as well as dasycladacean characteristics were integrated within this genus and postulated therefore a common phylogenetic stem of both families. He assigned *Palaeoporella* to the dasycladaleans (tribe Palaeoporelleae; cf. Shuysky, 1987: 71).

Palaeoporella seems to be a lower Palaeozoic genus, stratigraphically restricted from the Uppermost Cambrian to the Silurian (Stolley, 1893; Garwood, 1931; Johnson, 1954: 66; 1961: 100; 1966a: 21; 1966b: 28; Johnson *et al.*, 1959; Johnson & Hoeg, 1961; Jux, 1966; Kozlowsky & Kazmierczak, 1968a, b; Gnilovskaya, 1972; Saltovskaya, 1975; Wray, 1977: 81; Bourque *et al.*, 1981; Bassoullet *et al.*, 1983; Roux, 1985, Shuysky, 1987).

Elliott (1961) was the first to describe "remains of a small cylindrical alga with radiate structure" which "revealed to be a species of *Palaeoporella*", from Middle Devonian limestones (Torquay/Great Britain). As in most fossil udoteaceans, the medullary parts are poorly calcified, although Elliott (1961: 252) noted, that "the medullary cores show indistinct and irregular thin longitudinal threads".

Roux (in Bassoullet *et al.,* 1983: 554) pointed out, that the presence of numerous longitudinal threads as mentioned in specimens of *Palaeoporella lummatonensis* Elliott is not a characteristic of the genus *Palaeoporella.* So Mamet & Preat's (1985) decision to erect the new genus *Pseudopalaeoporella*, with *Palaeoporella lummatonensis* as type species, was justifiable. Later on, Shuysky & Shirshova (1987) erected the new monotypic genus *Funiculus* (with *Funiculus venosus* Shuysky & Shirshova), which is actually a *Pseudopalaeoporella* (Mamet & Preat, 1992: 55). A general synopsis of differences between *Palaeoporella* and *Pseudopalaeoporella* is given by Hubmann (1990: 150-151). Recently Vachard (1993: 93-97) discussed a possible synonymy of *Pseudopalaeoporella* with *Palaeoporella*, which is not followed here.

Pseudopalaeoporella lummatonensis (Elliott, 1961)
(Pl. I, Figs. 1-4)

1961 *Palaeoporella lummatonensis* Elliott, 251-254, Pl. 9, Figs. 1-5; Pl. 10, Figs. 1-4.
1983 *Palaeoporella lummatonensis* Elliott; Bassoullet *et al.*, 553-554, Pl. 13, Figs. 1, 2.
1985 *Palaeoporella lummatonensis* Elliott; Roux, 564.
1990 *Pseudopalaeoporella lummatonensis* (Elliott); Mamet & Preat, 441, Fig. 4.
1993 *Pseudopalaeoporella lummatonensis* (Elliott); Hubmann, 150-151, Pl. 35, Figs. 7-11.
1993 *Palaeoporella lummatonensis* Elliott; Vachard, 97-98, Pl. 6, Figs. 6, 18, 21-25.

Diagnosis: Calcified elongate-cylindrical thalli with circular cross-sections, differentiated into a cortical zone with irregular distally directed radiate fibres and a medullary zone with some fine filaments. The cortical filaments frequently branch dichotomously and usually widen strongly at their peripheral terminations, showing trumpet-like shapes at their distal endings (= the last dichotomous branch ing).

Description of the material: Within 18 thin-sections we studied some 500 various sections of segments. Generally the thalli are very well preserved, although silicification had somewhat affected the material. Nevertheless preservation makes some small detail apparent which support a medulla containing several fine filaments. Nevertheless the anatomy of the whole medullary zone still remains poorly known since calcification is too poor. The number of the central filaments remains indeterminable; it perhaps ranges between 12 and 18. External diameters of thalli range from 1.33-1.96 mm, usually about 1.6 mm. Length of (broken) fragments about 0.3-0.8 mm. Axial part of thallus diameter (medulla) 0.51-1.18 mm, usually about 0.78 mm.

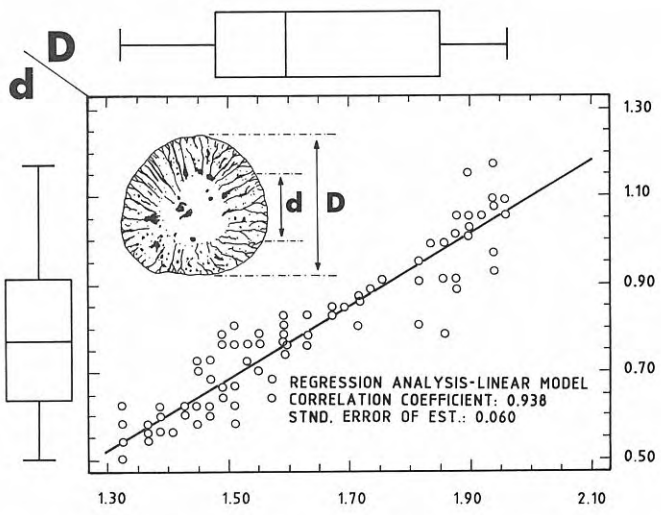
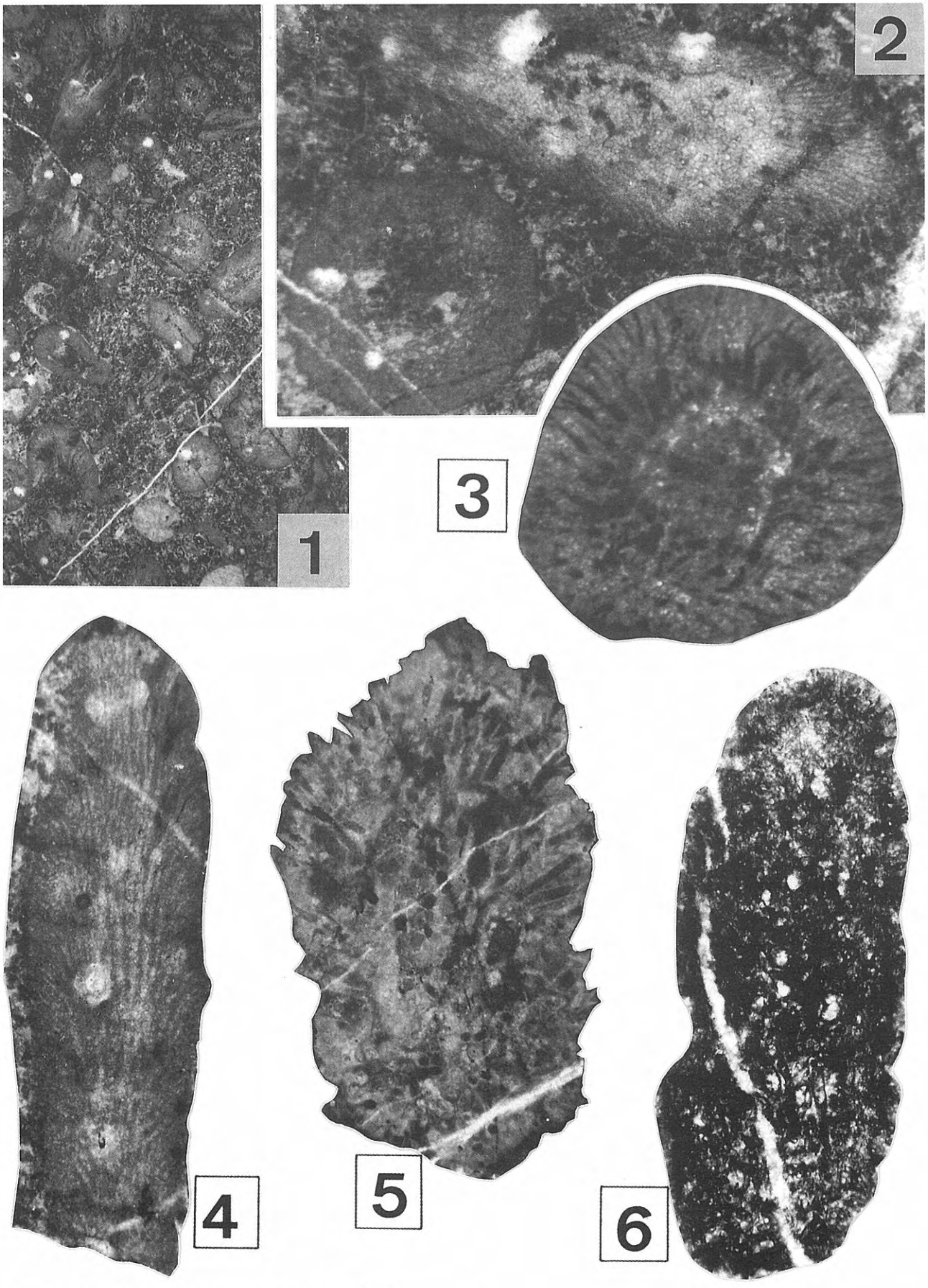


Figure 4. Biometric data of 100 measured specimens of *Pseudopalaeoporella lummatonensis* (Elliott, 1961). Box-and-whisker-plots for diameters of thalli (D) and medullas (d). Note significant linear correlation of d vs. D.

Plate I

1 Algal boundstones (bafflestones); 7 ×.
2 Transverse and longitudinal section of *Pseudopalaeoporella lummatonensis* (Elliott, 1961); 28 ×.
3 Cross-section of *Pseudopalaeoporella lummatonensis* showing several fine medullar threads and cortical filaments branching near the surface of the thallus; 38 ×.
4 Tangential longitudinal section of *Pseudopalaeoporella lummatonensis*; 24 ×.
5 Diagonal sectioned segment of *"Litanaia" graecensis* Hubmann, 1990; 18 ×.
6 Thallus of an unidentified udoteacean alga in longitudinal section; 21 ×.

Plate I



For detailed biometric data refer also to Fig. 4.

Discussion: The studied specimens closely fit the description and the biometric data sets of *P. lummatonensis* (cf. Elliott, 1961; Mamet & Preat, 1985; Hubmann, 1990). In the type-material the segments may reach a larger size, but that is not significant in udoteaceans, or in dasycladaleans.

Geographic and stratigraphic occurrence: Currently *Pseudopalaeoporella lummatonensis* is known from the Middle Devonian of the European realm (Elliott, 1961; Bassoullet *et al.*, 1983; Roux, 1985; Mamet & Preat, 1985; 1987; Preat & Mamet, 1989; Koch, 1989; Koch-Früchtl & Früchtl 1993; Koch-Früchtl & Gee 1994; Buggisch & Flügel, 1992; Hubmann 1990; Mamet & Preat, 1992): Torquay area/South-England, Wellin/Belgium, Berndorf/Germany (refer also to a remarkable finding of a Middle Devonian *"Palaeoporella"* mentioned by Pia (1924: 179) from the Rhenish Slate Mountains in the Eifel), the Urals (?) (Shuysky, 1987), Poland (A. Preat; pers. commun.) the Carnic Alps (Hubmann & Fenninger, 1993), Graz area/Austria (Hubmann, 1990, 1993) and the Armorican Massif (Vachard, 1993).

"Litanaia" graecensis Hubmann, 1990
(Pl. I, Fig. 5)

1990 *Litanaia graecensis* Hubmann, 140-150. Pl. 35, Figs. 1-6.

Diagnosis: Siphonous alga characterized by 4 to 12, generally 8, dichotomously branched filaments within the medulla. Thallus cylindrical and unsegmented; outer terminations of the thallus may show jagged boundaries.

Description of the material: In thin-section 109/1H a well preserved thallus exhibits four filaments within the medullary core, which is surrounded by a cortical zone with densely arranged fine threads. Diameters of medullar filaments vary about 0.21 to 0.27 mm, cortical filaments are about 0.062-0.094 mm in diameter. Diameter of thallus about 3.12 mm, medullar zone 1.25 mm in diameter. At the surface of the thallus, cortical filaments branch dichotomously. Because of blurred preservation due to diagenesis these tuning-fork shaped ramifications are often developed as triangular thickenings near the surface of the thallus.

Remarks: Unfortunately only one oblique section could be studied and therefore taxonomic assignment is uncertain; other specimens are too poorly preserved to allow better interpretations. Nevertheless the described specimen offers the essential characteristics of *L. graecensis* (cf. Hubmann, 1990: 148-149).

Discussion: Recently Mamet & Preat (in press) pointed out that some morphological characteristics of *"L." graecensis* differ from other representatives of *Litanaia* and proposed it as the type of a new genus.

Geographic and stratigraphic occurrence: At this stage *"L." graecensis* is only known from the Middle Devonian (Eifelian) of the Eastern Alps (Graz Palaeozoic) and from the Santa Lucía Formation at Geras de Gordón (this paper).

Gen. and sp. indet
(Pl. I, Fig. 6)

In some samples (109/1 A/1 B/1 C) thalli of a presumably udoteacean species are preserved in organic matter. Although cross-sections which reveal the internal anatomy (especially of the medulla) are not available, the cortical filaments can be perfectly studied due to the mode of preservation. They have striking similarities regarding fine structures with recent Halimedacea.

FLORISTIC AND PALAEOBIOGEOGRAPHIC RELATIONS

Siphonous algae (for instance *Litanaia* and *"Lanicula"*) were distributed worldwide within the intertropical climate zone during Devonian times as shown by Poncet (1982), Poncet & Blodgett (1987) and Hubmann (1990). This distribution seems to be more or less valid for the other udoteaceans as well (Poncet, 1990). Currently *Pseudopalaeoporella* is known from some localities in the European realm and its environmental settings also support an intertropical palaeoclimate. In addition, recent Udoteacean green algae show a characteristic clustering within the intertropical zone limited by the 25° C-seawater-isochryme. The 25° C- isochryme coincides approximately with latitude 30° N and S of the equator. Therefore, by analogy to recent conditions, the occurrence of the studied fossil green algae suggests a depositional environment inside the 25° C-isochryme within the "Rheic Ocean" (Hubmann, 1992). Also, the depositional basin of the Santa Lucía Formation did not extend beyond 30° S. Mutual floralgal relations on a species-level between Cantabria and the Graz area are quite remarkable. They suggest that both basins were interconnected. Moreover, connections with the ancient northern hemisphere (i.e. the Rhenohercynian basin) must also be postulated.

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