

Devonian Calcareous Algae of the South- and Austroalpine Region: The State of Knowledge

Devonische Kalkalgen aus dem süd- und ostalpinen Raum: eine Bestandsaufnahme

by

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We dedicate this work to Prof. Dr. H.W. FLÜGEL, who was the first to recognize Devonian Calcareous Algae in the Alpine region, on the occasion of his 70th birthday

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Abstract

Up to this decade palaeontologists have paid little attention to Devonian calcareous algae of the South- and Austroalpine Region. Consequently few systematic-taxonomic studies have been published, but, as we want to show, this is not at all related to any gap in their preservation. The findings generally show algal communities of low diversity and high numbers of individuals. At the present time we can recognize algae in many south- and austroalpine lithostratigraphic units.

Considering the different floralgal communities connected with microfacial parameters, we present preliminary distributional patterns of Devonian alpine algae in an environmental model.

Reliable biogeographical interpretations are only possible for the time span of the Upper Eifelian to Lower Givetian. They point out affinities of the Alpine areas with the Cantabrian Mountains, the Armorican Massif, the Dinant Basin, the Torquay area, the Eifel hills, Poland and the Urals.

Zusammenfassung

Der Kenntnisstand über devonische Kalkalgen aus dem süd- und ostalpinen Raum ist – im Vergleich zu devonischen Evertebraten, aber auch im Vergleich zur Kenntnis über Algen aus anderen Systemen, beispielsweise des Karbons oder Perms – recht bescheiden. Dies liegt aber **nicht** in der Tatsache begründet, devonische Kalkalgen hätten im alpinen Ablagerungsraum Überlieferungslücken (paläogeographische, -klimatologische, -latitudinale, -syn/autökologische Negativfaktoren, Taphonomie, Diagenese, etc.), oder seien auf statistische Einzelfunde beschränkt.

Erste Untersuchungen aus systematischen Aufsammlungen lassen erkennen, daß Algen horizontweise mit

großer Individuenhäufigkeit auftreten (können). Ebenso ist aus weiterführenden Untersuchungen zu erwarten, daß sie in flachmarinen Räumen der heutigen Süd- und Ostalpen weit verbreitet waren.

Nach unserem derzeitigen Wissensstand lassen sich aus folgenden devonischen Einheiten Kalkalgen belegen: Emsium bis Givetium des Grazer Paläozoikums, Emsium bis Givetium der Karawanken, Lochkovium bis Frasnium der Karnischen Alpen, sowie aus dem Eifelium der Gurktaler Decke (Abb. 1).

In Verbindung mit sedimentologischen/mikrofaziellen Daten kann aus den unterschiedlichen Algen-Assoziationen ein vorläufiges (paläo)geographisches Verteilungsmodell für das Devon alpiner Algen entwickelt werden (Abb. 2).

Floristische Bezüge (qualitativ wie quantitativ) herzu-leiten gelingen aufgrund des derzeitigen Datenstandes nur schwierig, obgleich mit *Pseudopalaeoporella lummatonensis* sowohl für das ost-, wie auch für das südalpine Mitteldevon (oberes Eifelium – unteres Givetium) Beziehungen zu benachbarten (peri)gondwanischen Terrains als auch zu Gebieten nördlich des „Rheia Ozeans“ beweisbar sind.

1. Introduction

In contrast to early Palaeozoic algae, a considerable number of articles dealing with Carboniferous and Permian algae is available (GORTANI, 1906; PIA, 1920, 1922, 1937; FLÜGEL, 1966; HOMANN, 1972; FLÜGEL & FLÜGEL-KAHLER, 1980). The fact that only little information on algae from the Devonian of the Alps is at hand is surprising, as there are many references to algal limestones in early articles. They all refer to “biolaminated rocks”(GERDES & KRUMBEIN, 1987) produced by the activity of “blue-green-algae” But obviously in most cases fine laminated carbonate rocks were – and still are! – assigned to stromatolites or

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microbial mats respectively, without checking their "algal" nature. We are aware of the possible misuse of the term "alga" for procaryote organisms (e.g. TORRES, 1991). Nevertheless we want to include them in the following excursus because of their photoautotrophic mode of life.

On the other hand, some forms were not recognized as algae; they were either ignored or assigned to other groups of organisms. *Zeapora gracilis* is a classic example from the Graz Palaeozoic: PENECKE (1894) described *Z. gracilis* as a cyclostomate Bryozoan. BASSLER (1953) considered *Zeapora* to be a representative of the Trepostomata and SOKOLOV (1955) assigned it with some restrictions to branching tabulate corals. Finally, H. FLÜGEL (1959) recognized *Zeapora*'s algal nature and assigned it to the Dasycladaceans (now: Dasycladaleans). More recent works are not cited so as not to single out some authors.

The algal flora from the Lower Devonian of the Carnic Alps described by PALLA (1965, 1966, 1967) and some references to *Girvanella* (Carnic Alps, Karawanken Mountains; SCHÖNLAUB, 1992; cum lit.) constituted the entire research in algae from the Devonian of the Eastern and Southern Alps until 1990.

Recent investigations show that algae are widespread in the Devonian of this area (HUBMANN, 1990; HUBMANN & FENNINGER, 1993; HUBMANN, 1994; and unpublished data). These results are based on samples taken in the Graz Palaeozoic, the Carnic Alps and the Karawanken Mountains, and on thin sections from the extensive collection of our institute at Graz. Although data of many south- and austroalpine lithostratigraphic units are now available, there still remain some regions with little information – or none at all –, e.g. the Greywacke zone and the Gurktal nappe (refer to Fig. 1).

Alpine Devonian calcareous algae, especially Dasycladaleans and Udoteaceans generally have a low diversity, but a large number of individuals. Algal thalli can be concentrated in well defined layers and make up the major part of the rock. If so, they are clearly visible in the field, when the rocks are well-weathered (HUBMANN, 1993a). This is true not only for alpine areas, but also, as we could see, for samples from the Eifel hills (FABER, 1980; LANGENSTRASSEN, 1993; HUBMANN & FENNINGER, 1994), the Cantabrian Mountains (HERRMANN & HUBMANN, 1994), the Chios Island and Turkey (FENNINGER, 1983).

Which floralgal elements can one expect in the alpine Devonian? We distinguish the following systematic groups:

* "microbial mats"

(Cyanobacteria, stromatolites and related forms)

* "Codiaceans"

* Udoteaceans

* Dasycladaleans

* Solenoporaceans

* Issinellids and Palaeoberesellids

* problematic algae

Issinellids and Palaeoberesellids are so far unreported in the alpine area. But, we have also to mention from the Carnic Alps (KREUTZER, 1990:287) the occurrences of *Devonoscalae* (see: LANGER, 1979; FLÜGEL in KREUTZER, 1990), which belongs in the opinion of some authors to these groups.

2. Some general remarks

Although the doubtful systematic position of individuals or groups of organisms and their possible assignment to algae or cyanobacteria plagues through the entire Phanerozoic, this is especially true for Precambrian and Early Paleozoic forms. This uncertainty concerns not only the question of an organism's attribution to the algae but also its position in the systematic framework. For example we may cite the *Wetheredella*-group: they are systematically assigned to Chlorophyta, Microproblematics, Foraminifers or worms (CHUVASHOV & RIDING, 1984).

There are also uncertainties concerning the genera *Epiphyton* and *Renalcis*. On one hand they are regarded as one single group of "coccooid blue-green algae", and their "genus- and species-specific distinctive marks" are attributed to diagenetic processes (PRATT, 1984). On the other hand they are regarded as independent genera of cyanobacteria (*Epiphyton*: an assignment to Rhodophyta is discussed). In this case they are split into a large number of species, hardly comprehensible and poorly distinguished. The systematic position of the following genera abundant in the Devonian is also unclear: *Bevocastria*, *Ortonella*, *Hedstroemia*, and *Garwoodia*. Referring to PIA's (1927) systematic concept they are assigned to Porostromates. Referring to JOHNSON (1961) they are assigned to filamentous Codiaceans. None of the assignments are accepted without reservations.

Another problem area concerns the definition of genera, especially the characteristic Devonian udoteacean genus "*Lancicula*" (cf. HUBMANN, 1993b).

Something similar happens with "*Litanaia*":

– Splitting up in several genera (SHUYSKY & SHIRSHOVA, 1988, MAMET & PREAT, 1985, 1992)

– Attempting to resolve the problems on the base of a subgenus (MAY, 1992)

– Maintaining one single genus (VACHARD, 1993)

There are also uncertainties concerning different degrees of calcification among Udoteaceans that have a systematic importance (PIA, 1920; JOHNSON, 1961).

The best example is *Pseudopalaeoporella lummatonensis*: 1893: STOLLEY establishes the genus *Palaeoporella* from Ordovician strata of Scandinavia. He defines this genus, among other factors, by the existence of a single medullar tube: „Von der centralen Stammzelle der Körper..." (STOLLEY, 1893:137). He

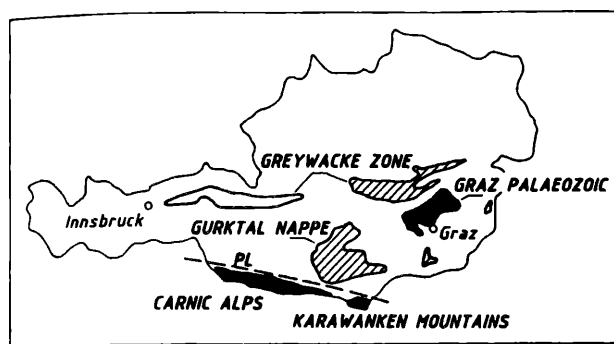


Figure 1: Distribution of Palaeozoic non-metamorphic rocks of Austria. At this stage the best results on calcareous algae originate from areas coloured in black. Only little information is available from hatched and none from uncoloured areas. PL ... Periadriatic lineament

assigns the genus to the Dasycladaceans.

1927: PIA assigns the genus *Palaeoporella* to the Codiaceans.

1961: ELLIOTT describes *Palaeoporella lummatonensis* from the Devonian of Torquay and assigns this new species to the Codiaceans. He suspects medullar filaments, only visible in a few traces because of diagenetic processes. BOURQUE et al. (1981) also refer to this phenomenon.

1961: JOHNSON regards *Palaeoporella* as a genus of Codiaceans, which are today united under Udoteaceans. JUX (1966), KOZLOWSKI & KAZMIER-CZAK (1968) and WRAY (1977) follow this idea.

1968: HURKA examines *Palaeoporella variabilis* from the Ordovician of Norway (Ringerike, Fragnoen). He largely corroborates STOLLEY's observations. He regards this genus as a representative of Dasycladaceans and establishes the new tribus Palaeoporelleae (cf. also SHUYSKY in SHUYSKY & SHIRSHOVA, 1987).

1985: MAMET & PREAT establish the genus *Pseudopalaeoporella*. Generotype is *Pseudopalaeoporella lummatonensis*. They base the establishment of a new genus in the existence of medullar filaments (cf. also HUBMANN, 1990).

1987: SHUYSKY & SHIRSOVA describe a new Udoteacean genus with *Funiculus venosus*. It has the same cortical construction as *Pseudopalaeoporella*, but is distinguished by a clearly developed medulla.

1992: MAMET & PREAT recognize the same phenomenon on Devonian specimens from Belgium. They conclude that *Funiculus* is a more recent synonym for *Pseudopalaeoporella*.

1993: VACHARD assigns *Pseudopalaeoporella lummatonensis* once again to *Palaeoporella* and assigns the genus to the green or red algae (sic!).

1993: HUBMANN & FENNINGER corroborate MAMET & PREAT's idea. They regard *Pseudopalaeoporella* as a representative of Udoteaceans and confirm the synonymy of *Funiculus*.

3. Distributional framework and data base

(1) Graz Palaeozoic

We have good results from carbonate rocks of the higher nappes of this Palaeozoic complex. These are the Hochlantsch- and the Rannach Nappe; at this time, the latter brings better results.

The Dolomite-Sandstone-Formation developed in both nappes often includes layers of microbial mats (sometimes with tepee structures) and subordinate till now not determined Dasycladaceans in the light and dark dolomite members of the formation (FENNINGER & HOLZER, 1978). The latter is rich in elements which we put for the moment into the calcisphere group. They are mainly present in lagoonal milieux (for instance in the "Middle devonian Dolomites"). But they are also found in other environments of the entire lower and middle Devonian of the Graz Palaeozoic (Fig. 2).

The green algae flora is beautifully represented in the Barrandei-Limestone (HUBMANN, 1990). They are mostly found in well defined layers of marly nodular limestones. We regard these layers as algal meadows, wherein *Zeapora gracilis* or *Pseudopalaeoporella lummatonensis* and *Litanaia graecensis* are dominant (HUBMANN, 1993a).

(2) Carnic Alps

Following the taxonomic studies on "Codiaceans" and Udoteaceans by PALLA (1965, 1966, 1967), HUBMANN & FENNINGER (1993) and HUBMANN (1994) and the microfacial investigations of KREUTZER (1990, 1992) we can detect algae in all shallow marine Devonian units of the central part of this chain.

A significant facies-sensitive community depending on the depositional environment becomes apparent when one compares algal associations of different lithostratigraphic units. In contrast to the Graz Palaeozoic with its green algae, an association of Codiaceans and Udoteaceans is developed in lower Emsian limestones. PALLA described a flora of *Garwoodia volaiensis*, *Ortonella* sp., *Litanaia maslovi* (which is a *Paralitanaia*), *Lancicula gortanii* (which is a *Lanciculella*) and *Lancicula wolffi* (which is a *Quasilancicula*).

From the Lochkovian of the neritic Rauchkofel limestone we described the oldest Udoteacean species of Austria: *Paralitanaia carnica*, which appears together with *Quasilancicula wolffi* ? and *Lanciculella gortanii* ? (HUBMANN, 1994).

The Feldkogel-Limestone also shows a typical community: in addition to microbial mats, calcispheres, parathuraminids and other problematic algae could be recognized. From the Kellergrat-Reef-Limestone KREUTZER (1990, 1992) mentioned *Renalcis turbitus* (= *R. granosus* after MAMET & ROUX, 1983, = *R. nubiiformis* after VACHARD, 1993). Here a typical *Renalcis* or a *Renalcis-Solenopora*-community associated with stromatoporoids and corals is developed. KREUTZER

(1990, 1992) also reports occurrences of *Devonoscalae tatarstanicae* from the pelagic Cellon-Limestone and dasycladacean remains from the Eiskar-Limestone. The systematic taxonomy of the latter will be studied in detail through our project on Devonian algae.

(3) Karawanken Mountains (Seeberg Aufbruch)

In the Karawanken Mountains, algae are known from the Devonian reef and algal limestones (with *Girvanella*) of the Seeberg-Aufbruch (TESSEN SOHN, 1974). From the microfacial point of view there is a good correspondence between the Devonian shallow water successions of the Carnic Alps and those of the Karawanken Mountains (RANTITSCH, 1992). But there is a disparity in quantity of calcareous green algae. The reason for the lower number of algae in the Karawanken Mountains seems to be taphonomic rather than ecologic. As in the Kellergrat-Reef-Limestone (KREUTZER, 1990, 1992) of the Carnic Alps, *Renalcis* is associated with stromatoporoids and corals (RANTITSCH, 1992). In addition it is possible to detect a "Codiacean"-Dasycladalean-community. But until now, only a few badly preserved specimens have been found.

(4) Other regions

We could detect *Pseudopalaeoporella lummatonensis* from Tertiary conglomerates (Arnfels conglomerate) of reworked Palaeozoic boulders. These boulders supposedly originate from the Palaeozoic of the Possruck area, which is in some authors' opinion assigned to the Gurktal Thrust System. The latter contains according to SCHÖNLAUB (1971) remains of dasycladaleans in the "Althofen Biogenschuttkalke" (Eifelian) at Althofen (Aich outcrop). Unfortunately we could not prove their existence, although we have resampled the locality; we did, however, recognize some Solenoporaceans.

The anchimetamorphic to epizonal Crinoid-Stromatoporoid Formation of the Polster profile (Greywacke Zone of Styria) (SCHÖNLAUB, 1992 cum lit.) includes dark carbonaceous layers, which are rich in forms of the *Epiphyton*-Group.

4. Environmental model

Devonian floralgal communities in the South- and Austroalpine Domain indicate different depositional environments, which are also based on microfacies (refer to Fig. 2):

- (1) Microbial mats in connection with tepee structures are assigned to an intertidal to supratidal environment.
- (2) The lagoonal facies is characterized by a near-shore Codiacean-Udoteacean-community and a Dasycladalean-Udoteacean-community in the back-reef area. A third lagoonal association is represented by calcispheres and other problematic "algae".

Associations of amphipores, calcispheres, etc. are often regarded as an indicator for abnormal marine conditions (e.g. FLÜGEL & HÖTZL, 1971; KAZMIERCZAK, 1976)

- (3) We assign the *Renalcis*- and the *Renalcis-Solenopora*-community to the central reef facies. Here *Renalcis* and related forms together with coelenterates have a framework-building function.

A comparable assemblage, also found in high energy Holocene reefs, is known in Polynesia (MONTAGIONI & CAMOIN, 1993).

5. Palaeobiogeographic considerations

At this stage we do not have enough data from the whole Devonian system for a reliable biogeographical interpretation. Therefore our statement presented on this topic should be regarded as preliminary. Considering that the systematic taxonomy of Devonian green algae has become more and more sophisticated, it is advisable to restrict comparison at the species level. For instance *Pseudopalaeoporella lummatonensis* is currently known from Upper Eifelian to Lower Givetian localities in the European realm: the Torquay area (SW-England), the Eifel hills (Germany), the Dinant Basin (Belgium), the Armorican Massif (NW-France), the Cantabrian Mountains (N-Spain), Poland and (presumably) the Urals (ELLIOTT, 1961; MAMET & PREAT, 1985, 1992; HUBMANN, 1990, 1992; VACHARD, 1993; SHUYSKY in SHUYSKY & SHIRSHOVA, 1988; HUBMANN & FENNINGER, 1993; HERRMANN & HUBMANN, 1994). The (peri-)gondwanian occurrences indicate that the basins of the Aquitaine-Cantabrian-terrain and the terrains of the Carnic Alps and the Graz Palaeozoic were interconnected during Middle Devonian times. Furthermore there existed a connection with Laurussian areas.

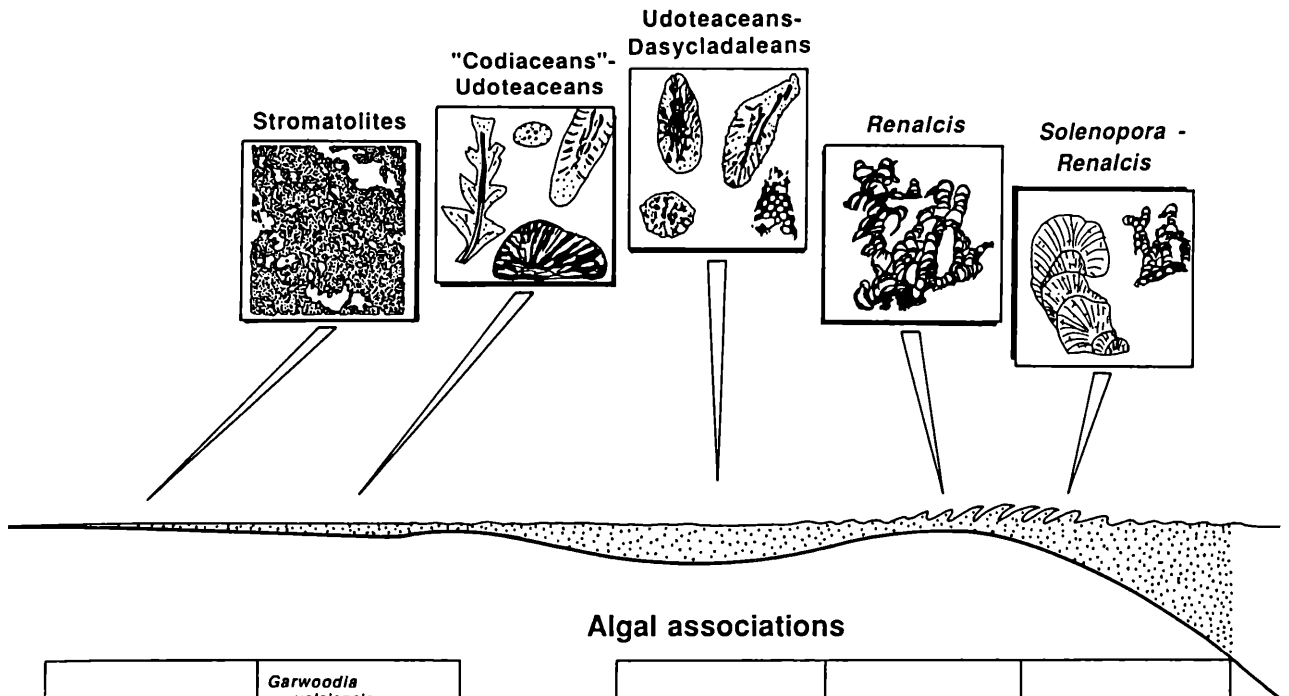
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Algal associations

"microbial mats"	<i>Garwoodia volalensis</i> <i>Garwoodia</i> sp. <i>Ortonella</i> sp. <i>Parallitana carnica</i> <i>Parallitana maslovi</i> <i>Parallitana</i> sp. <i>Pseudopalaeporella lummatonensis</i> <i>Lanciculella gortanii</i> <i>Quasllancicula wolff</i>	<i>Pseudopalaeporella lummatonensis</i> <i>Litanala graecensis</i> <i>Zeapora gracilis</i>	<i>Renalcis "granosus"</i> <i>Renalcis</i> sp.	<i>Solenopora</i> sp. <i>Renalcis</i> sp.

Lithostratigraphic units / areas

Dolomitsandstein-Fm. Barrandel-Lmst. "Middledevonian Dolomites" Piatzkogel-Lmst. Tyrnaueralm-Fm.			Dolomitsandstein-Fm. Barrandel-Lmst.			Graz Palaeozoic
Gamskofel-Lmst. Lambertenghi-Lmst. Feldkogel-Lmst.	Rauchkofel-Lmst. (neritic facies) Hohe Warte-Lmst. Spinotti-Lmst. Marinelli-Lmst.	Spinotti-Lmst.	Eiskar-Lmst. Spinotti-Lmst.	Kellergrat-reeflimestone	Kellergrat-reeflimestone	Carnic Alps
"Algal limestones"	"Reef limestone"		"Reef limestone"	"Reef limestone"		Karawanken Mountains

Figure 2: Distribution of Alpine Devonian algal associations along an idealized profile of a carbonate shelf margin.

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