Upper Palaeozoic Bryozoa in Carnic Alps, Austria (a review)

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Abstract: The aim of this article is to outline the distribution of bryozoans in Upper Palaeozoic rocks of Carnic Alps, Austria. The richest occurrences of bryozoans were documented in the Upper Carboniferous Auernig Formation (literature data), and in the Lower Permian Trogkofel Formation (own results). Less diverse and abundant bryozoan faunas are known from other units of the Upper Carboniferous – Lower Permian sequence of Carnic Alps. Bryozoans show distinct biogeographical connections to contemporary faunas from Urals, Caucasus, and Australia.

Key words: Upper Palaeozoic, Bryozoa, Carnic Alps, taxonomy, biogeography.

Introduction

Palaeozoic Bryozoans belong mostly to the class Stenolaemata. Only few taxa represent the class Gymnolaemata, and their importance in Palaeozoic rocks is negligible. Representatives of the class Phylactolaemata possess no calcitic skeleton; so far their fossil record is almost unknown. Only their cysts, or statoblasts, are known at least from Mesozoic. Stenolaemate bryozoans appeared in the Lower Ordovician having apparently long hidden evolution since Cambrian. They acquired calcitic skeletons which made possible their quick radiation. The most of Palaeozoic orders died out at the end of Permian age, some few genera survived until the Late Triassic. Apparently only one group (order Cyclostomida) could survive until today, although their relations to other bryozoan clades are not completely understood.

Upper Palaeozoic Bryozoa were investigated in Carnic Alps in course of the DFG-project "Systematics and Phylogeny of the Bryozoans of the Permian in Europe: Importance for Biogeography and Ecology in German Zechstein Basin and in the NW-Tethys" (Scha 355/13-1 u. 2). This study included investigation of bryozoan samples from Upper Palaeozoic (Upper Carboniferous – Lower Permian) rocks of Carnic Alps.

The investigated material was sampled during field works 1995-1997 in the Carnic Alps, along the Austrian/Italian border (Fig. 1). Bryozoans were found in rocks of Corona (Corona), Lower *Pseudoschwagerina* (Ringmauer), Upper *Pseudoschwagerina* (Garnitzenbach, Zweikofel), and Trogkofel (Garnitzenbach and Trogkofel) formations. For the taxonomic descriptions more than 200 thin sections were produced.

Previous investigations

Upper Carboniferous bryozoans of the Carnic Alps have only occasionally been studied. JOHNSEN (1906) described 33 bryozoan species from the Auernig Formation (bed "s"), mostly fenestrate taxa. However, this fauna needs to be re-studied. Later, CERETTI (1963, 1964, 1967) described in all 54 bryozoan species from the bed "l" of the Auernig Formation. Most of these descriptions were performed without using thin sections which are necessary for exact identification of Palaeozoic bryozoans. The Lower Permian bryozoans of the Carnic Alps were only recently investigated (ERNST 2000, 2001, 2002, 2003). These studies showed an unexpected high bryozoan diversity in some formations of the Lower Permian. Nevertheless, our general knowledge about Upper Palaeozoic bryozoans of Carnic Alps is still very fragmentary.

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Fig. 1: Location of investigated profiles in Carnic Alps, Austria.

Methods

Palaeozoic bryozoans are usually embedded in solid rocks. They reveal also many important interior characters invisible from the colony surface. Therefore, an investigation of Palaeozoic bryozoans requires using of thin sections. For this aim rock pieces are sawed with a concentric diamond-saw in smaller fragments. Plain surfaces are polished on polishing machines by using polishing powders. Thin slabs from polished surfaces are formatted to fit object-glasses. In the next step dry and fat-less polished surfaces of slabs are glued by an epoxide resin or Canada-balsam on object-glasses. The slabs are cut away using special machines and leaving only a thin layer on the glass. This layer is still 100-200 µm thick. Other machines are used for polishing of thin sections until the rock slab on the glass is about 30-35 µm thick. This slab is transparent enough to see details of inner structure of organisms. Usually, thin sections are covered by an additional thin glass slab in order to protect surface and to get better optical quality.

Another method to get information about an interior structure of bryozoans is using of so-called acetate peels. Polished carbonate samples are etched shortly by weak acid, usually chloride or amic acid. The etched surface reveals a distinct relief because of a different solubility of the rock components such as mineral crystals, skeletal elements and matrix. Dry etched surface is poured by acetone and covered by a special plastic film which is soluble in acetone. After 10-15 minutes the film becomes hard, and can be drawn from the sample. Thin films should be immediately pressed between two glasses, e.g. in a slide frame. The quality of acetate peels can be better than thin sections, but depends on a composition of the rock. Some examples of acetate peels are on the Figures 6a, c, f, g, i.

An investigation of bryozoan thin sections requires special orientations of the colony. Usually these are tangential section (parallel to the colony surface), cross section (perpendicular to the branch), and longitudinal section (along the branch) (Fig. 2).

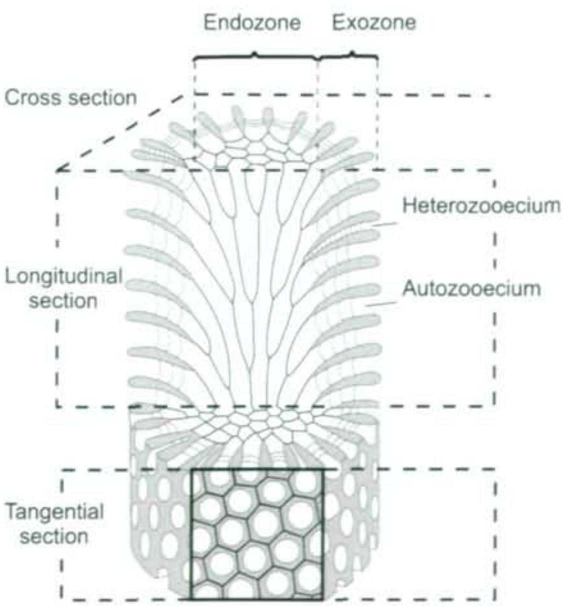

Fig. 2: Position of sections used in investigation of Palaeozoic Bryozoa.

Stratigraphy and lithology

The Upper Palaeozoic carbonate sequence in the Carnic Alps starts in the Upper Carboniferous (Fig. 3). The uppermost Carboniferous beds are correlated to the *Ultradaixina bosbytaensis-Schwagerina robusta* fusulenacean zone of the Southern Urals. The Carboniferous/Permian boundary is placed in the uppermost part of the Lower *Pseudoschwagerina* Formation, near the base of the overlying Grenzland Formation (FORKE et al. 1998).

The Corona Formation predominantly consists of clastic sediments deposited in the nearshore environment, intercalated locally by silts and shales, as well as fossiliferous limestones. The limestones contain a rich fauna of calcareous algae, fusulinids, small foraminifers, echinoderms, and bryozoans. The age of the Corona Formation is regarded as Late Gzhelian (KRAINER & DAVYDOV 1998).

The Lower *Pseudoschwagerina* Formation displays four cyclothems (SAMANKASSOU 1997), as a follow of a cyclic sedimentation in nearshore area. Rocks of this Formation are represented predominantly by biomicritic limestones containing calcareous algae, foraminifers, gastropods, echinoderms, and bryozoans. The age of the Lower *Pseudoschwagerina* Formation is provided by foraminifers as Late Orenburgian.

The Upper *Pseudoschwagerina* Formation displays an alteration of thin to intermediate bedded limestones with rare clastic intercalations (Fig. 4). Clastic sediments are quarz-rich conglomerates and sandstones. This formation was deposited on an open shelf (BUTTERSACK & BOECKELMAN 1984). The limestones contain abundant fossils: predominantly calcareous algae, brachiopods, gastropods, crinoids, echinoids, foraminifers, and bryozoans. The age of the Upper *Pseudoschwagerina* Formation was defined as Sakmarian (FORKE 1995; KRAINER & DAVYDOV 1998).

The Trogkofel Formation consists of massive carbonates (Fig. 5). Two facies were defined here by FLÜGEL (1981): 1) coloured and white reef limestones with *Archaeolithoporella* and *Tubiphytes*; 2) bedded limestones, which present an extension of the platform facies. The age of the Trogkofel Formation is as Late Sakmarian to Early Artinskian (FORKE 1995). Diverse fossils such as fusulinids, brachiopods, crinoids etc. occur in the Trogkofel Formation.

Distribution of bryozoans in Upper Palaeozoic of the Carnic Alps

Bryozoans are unevenly distributed in rocks of the Upper Palaeozoic in Carnic Alps. They belong mainly to orders Cystoporida, Trepostomida, Rhabdomesida, and Fenestellida (Tab. 1). The richest occurrence of Upper Carboniferous bryozoans in Carnic Alps is restricted to the Auernig Formation (JOHNSEN 1906; CERETTI 1963). In the Corona Formation and Lower *Pseudoschwagerina* Formation bryozoans are ubiquitous, but mostly presented as fragments and not very abundantly fauna (FLÜGEL 1974, 1987; SAMANKASSOU 1997; FORKE et al. 1998). Only one species, *Rhombocladia delicata* ROGERS 1900, was identified from the Corona Formation. Some few bryozoans species were found in the Lower *Pseudoschwagerina* Formation: *Streblotrypa* (*Streblotrypa*) sp., *Clausotrypa monticola* (EICHWALD 1860) (Fig. 6e), and *Hayasakopora schaefere* ERNST 2003.

In the Lower Permian (Sakmarian) Upper *Pseudoschwagerina* Formation bryozoans are rare. Following taxa were identified here: *Eridopora* sp., *Prismopora digitata* CROCKFORD 1957 (Fig. 6n-o), *Tabulipora* sp., *Alternifenestella tenuiseptata* (SCHULGA-NESTERENKO 1941), *A.* aff. *tenuiseptata* (SCHULGA-NESTERENKO 1941), and *A. nalivkini* (ELIAS & CONDRA 1957).

The overlaying Trogkofel Formation (Sakmarian - Artinskian) displays a richer bryozoan diversity. The following taxa occur in the *Archaeolithoporella-Tubiphytes* facies: *Eridopora ignota* GORJUNOVA 1975, *Eridopora* sp., *Prismopora* sp., *Goniocladia* sp., *Stenophragmidium lamellatum* ERNST 2003 (Fig. 6a-d), *Streblascopora germana* BASSLER 1929, *Primorella serena* GORJUNOVA 1975 (Fig. 6j-l), *Rhabdomeson hirtum* (CERETTI 1963) (Fig.

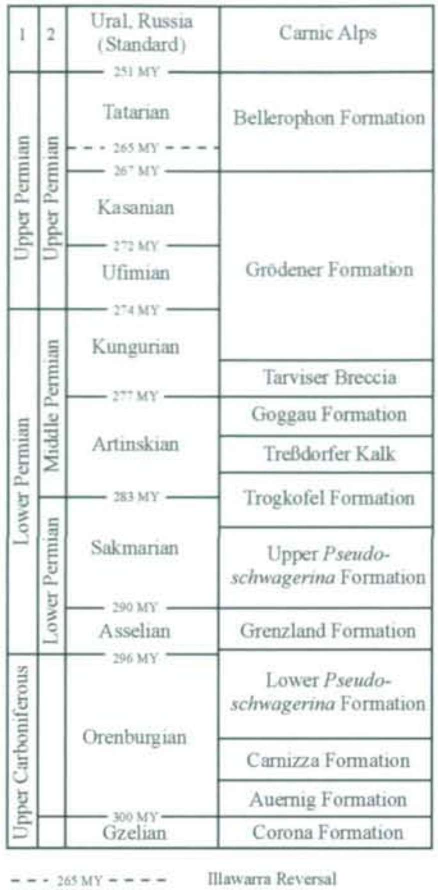

Fig. 3: Stratigraphy of Upper Palaeozoic rocks in Carnic Alps (compiled after FORKE 1995; KRAINER & DAVYDOV 1998; without scale).

Fig. 4: Locality Zweikofel outcropping rocks of the Upper *Pseudoschwagerina* Formation (Lower Permian, Sakmarian).

Fig. 5: Locality Trogkofel outcropping rocks of the Trogkofel Formation (Lower Permian, Sakmarian – Artinskian).

6f-g), *Penniretepora trapezoida* NIKIFIROVA 1938, *Penniretepora* spp., *Alternifenestella subquadratopora* SCHULGA-NESTERENKO 1952, *A. tuberculifera* SCHULGA-NESTERENKO 1952 (Fig. 6m), *Polypora sigillata* GORJUNOVA 1975, *Paraptylopora* sp. (Fig. 6h), *Carnocladia fasciculata* ERNST 2001 (Fig. 6i), and *C. punctata* ERNST 2001.

Biogeographical implications

Accomplished studies displayed high richness and diversity of bryozoan faunas in the Upper Palaeozoic of Carnic Alps. Bryozoan faunas in neighbouring areas are also very scarcely investigated. Only few publications regard the Upper Carboniferous bryozoans of the European region: ZÁGORČEK (1993), DELVOLVÉ & MCKINNEY (1983), and GONZÁLEZ & SUARÉZ (1999).

The new data allow an improved analysis of a bryozoan distribution in the Upper Palaeozoic of Europe. The species *Prismopora digitata* CROCKFORD 1957 displays a connection to the Lower Permian of Australia. However, the bulk of the abundant and diverse bryozoan fauna from the Trogkofel Formation shows strong connections to the contemporary fauna from SW Darvaz and Urals. So that, they generally support results achieved using other groups such as fusulinids (ROSS 1995; FORKE 1995; KRAINER & DAVYDOV 1998). A similarity in bryozoan faunas displays an existence of a connection between the Tethys and the Uralian Sea at least up to the Early Artinskian. This connection has closed during the Early Permian. Fusulinid faunas, however, displays another pattern. KRAINER & DAVYDOV (1998) support an idea that exchange in fusulinid faunas stopped earlier – before Sakmarian. This fact could also be explained by different ecological claims of bryozoans and fusulinids regulating the faunal distribution. Both bryozoans and fusulinids represent benthic groups. They does not claim necessary on light like corals or algae but need enough nutrient supply. Bryozoans occur usually in near-shore conditions, whereas fusulinids are fixed to clear waters of shallow open-sea areas. Additionally, their larvae could reveal different strategies of distribution. Apparently, Palaeozoic bryozoans have had long-living larvae because evidences of brooding structures are very scarce in them (except, maybe, fenestrate bryozoans). Such

Tab. 1. Taxonomic assignment of Upper Palaeozoic bryozoans from Carnic Alps.

Class Stenolaemata			
Trepostomida	**Cystoporida**	**Fenestrida**	**Cryptostomida**
Tabulipora sp.	*Prismopora digitata* CROCKFORD 1957	*Alternifenestella tenuiseptata* (SCHULGA-NESTERENKO 1941)	*Streblascopora germana* BASSLER 1929
Stenophragmidium lamellatum ERNST 2003	*Prismopora* sp.	*A.* aff. *tenuiseptata* (SCHULGA-NESTERENKO 1941)	*Streblotrypa* (*Streblotrypa*) sp.
	Eridopora ignota GORJUNOVA 1975	*A. nalivkini* (ELIAS & CONDRA 1957)	*Rhabdomeson hirtum* (CERETTI 1963)
	Eridopora spp.	*A. subquadratopora* SCHULGA-NESTERENKO 1952	*Clausotrypa monticola* (EICHWALD 1860)
	Goniocladia sp.	*A. tuberculifera* SCHULGA-NESTERENKO 1952	*Hayasakopora schaefere* ERNST 2003
		Penniretepora trapezoida NIKIFIROVA 1938	
		Penniretepora spp.	
		Polypora sigillata GORJUNOVA 1975	
		Paraptylopora sp.	
		Carnocladia fasciculata ERNST 2001	
		C. punctata ERNST 2001	
		Rhombocladia delicata ROGERS 1900	

larvae were able to get over areas of unfavourable conditions.

Investigated bryozoan faunas from the Upper Palaeozoic of Carnic Alps contain a low number of endemic species. Only the genus *Carnocladia* ERNST 2003 of a family Carnocladiidae ERNST 2003 seems to be completely endemic to this region, maybe also occurring in contemporary sediments of Spain. That is apparently a general trend characteristic for different faunal groups of this age indicating an intensive faunal exchange. Otherwise, many Upper Palaeozoic faunas from European region remain unstudied. New investigations are required for understanding of distribution, diversity dynamics, and evolution of bryozoans in Late Palaeozoic of Europe.

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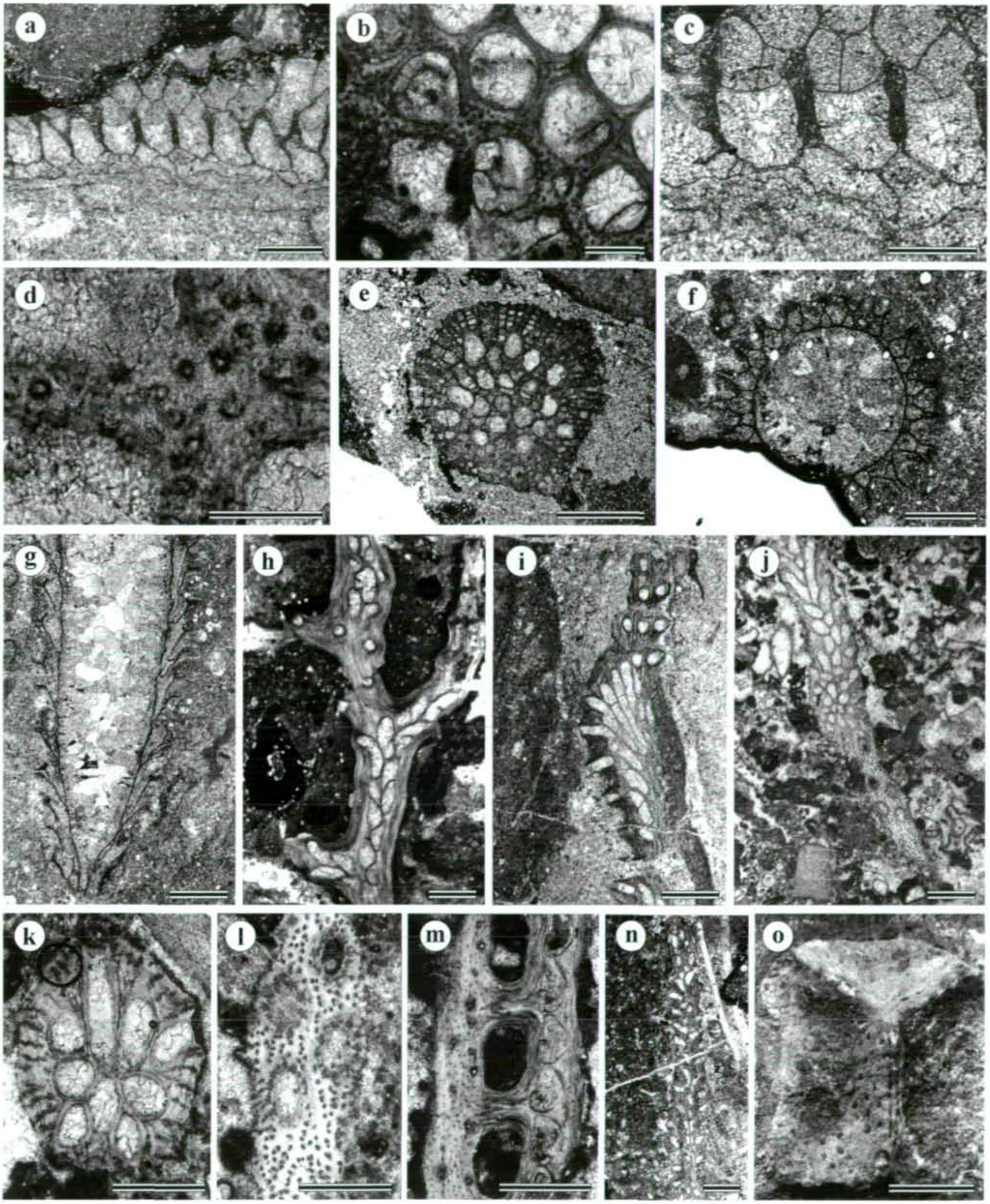

Fig. 6: *Stenophragmidium lamellatum* ERNST 2003 (a-d), *Clausotrypa monticola* (EICHWALD 1860) (e), *Rhabdomeson hirtum* (CERETTI 1963) (f, g), *Paraptylopora* sp. (h), *Carnocladia fasculata* ERNST 2003 (i), *Primorella serena* GORJUNOVA 1975 (j-l), *Rectifenestella tuberculifera* (SCHULGA-NESTERENKO 1952) (m), and *Prismopora digitata* CROCKFORD 1957 (n-o). **a**: longitudinal section (peel), scale bar = 0.5 mm; **b**: tangential section, scale bar = 0.25 mm; **c**: longitudinal section (peel), scale bar = 0.25 mm; **d**: tangential section displaying microacanthostyles, scale bar = 0.1 mm; **e**: cross section, scale bar = 1 mm. **f**: cross section (peel), scale bar = 0.5 mm; **g**: longitudinal section (peel), scale bar = 1 mm; **h**: tangential section, scale bar = 0.5 mm; **i**: separate branch (peel), scale bar = 1 mm; **j**: separate branch, scale bar = 1 mm; **k**: cross section of the branch, scale bar = 0.5 mm; **l**: tangential section, scale bar = 0.5 mm; **m**: scale bar = 0.5 mm; **n**: longitudinal section, scale bar = 1 mm; **o**: colony surface, scale bar = 1 mm.