LATE EOCENE BRYOZOAN FAUNAS IN THE ALPINE-CARPATHIAN REGION - A COMPARISON

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Abstract. Twelve Priabonian (Late Eocene) bryozoan faunas of the Alps and Carpathians, collected from shallow to deep marine sediments, are compared by similarity indices. High-diversity faunas from shallow bathyal bryozoan marls, where zoaria occur in rock-forming quantity, display the highest similarity - common for deep-water biota - despite their palaeogeographic position on widely separated terranes. Lower-diversity shallow marine faunas reflect less favourable conditions for bryozoan growth.

Keywords: Eocene, Bryozoa, Alps, Carpathians, and paleogeography.

INTRODUCTION

Comparing fossil faunas for the purpose of understanding plate tectonic processes have been a favourite pastime of palaeontologists since the pioneer syntheses in HALLAM (1973). Displacement history of exotic terranes along the Pacific margins of America was described in increasing detail based on comparing fossil faunas (e.g. WESTERMANN, 1984; HOWELL, 1985). Gondwanian or Asian origin of terranes in the Tethys was determined by comparing the faunas they carried (AUDLEY-CHARLES & HALLAM, 1988). Beyond these continental-scale studies it is possible to describe the displacement history of minor terranes (e.g. Apulia in the Tethys: VÖRÖS, 1993, by brachiopods) and to recognise the nature of barriers to faunal migration (e.g. ammonites of the Mediterranean: GÉCZY, 1986).

Studies on Palaeozoic and Mesozoic faunas seem to yield more spectacular results due the longer duration of time available for tectonic processes to displace them (HALLAM, 1994). However, a recent recognition of significant Miocene tectonic displacements in the Alpine range between the Alps and Anatolia (KÁZMÉR & DUNKL, submitted) called our attention to the possibility of Tertiary palaeobiogeographic analyses of the region. Palaeolatitude determination of several terranes (KÁZMÉR et al., 1999) allowed to recognise the great width of the Paratethys ocean extending between the southern shelf of Europe and the northern margin of the Alpine orogen. This basin, extending across more than 10 degrees in latitude, probably extended across climatic belts, which established the necessary conditions for the provinciality of several organisms (KÁZMÉR, 1999).

This paper is the first in a series in which we attempt to document biogeographic similarities and dissimilarities of faunas and floras in the Tertiary Paratethys region, and offer possible explanations for their causes in a plate tectonic context.

BRYOZOANS

The Alpine-Carpathian region probably hosts the best described Paleogene bryozoan faunas of the world. The first author described several of them, studied museum collections and checked published monographs (for details see localities). An initial study compared the faunas of six localities (BRAGA et al., 1996). The present paper contains data on twelve faunae altogether and - using the same statistical method as BRAGA et al. (1996) - analyses similarity coefficients in a realistic palaeogeographic framework.

Lithology of the embedding sediment

Late Eocene bryozoans in the Alpine-Carpathian region occur in three major groups of sediments. Bryozoan marl contains the most diverse bryozoan association. A less diverse one is hosted by bioclastic marl with larger foraminifers and corallinacean algae. Also, bryozoans can be common components in fine-grained calcareous sandstone.

Bryozoan marl

A marl rich in bryozoan zooecia has been first found by HOFMANN (1871) in the Priabonian of Buda Hills, Hungary. Its occurrence in many Carpathian localities has been recognised since his times.

The bryozoan marl contains more than 30 weight percent of bryozoan zoaria. The fauna consists of more than hundred bryozoan species (mostly Cheilostomata of erect growth form), a small amount of echinoid fragments, planktonic foraminifers, and small shells of the brachiopod *Argyrotheca*.

Localities with described bryozoan faunas are:

- Mátyáshegy, Budapest, Hungary (ZÁGORŠEK & KÁZMÉR, in press).
- Hybica and Štrba, Liptov basin, Slovakia (ZÁGORŠEK, 1992, 1994, 1997)
- Brendola, Brentonico and Pannone, Southern Alps, Italy (BRAGA, 1963, 1965)
- Cluj-Napoca, Transylvanian basin, Romania (PERGENS, 1887; KOCH, 1894)
- Helmberg 1 borehole, Salzburg, Molasse basin, Austria (ZÁGORŠEK, in preparation).

The bryozoan marl usually occurs in a deepening-upward sequence. The succession starts with bioclastic limestone with corallinacean algae and larger foraminifers, up to 100 m thick, overlain by *Discocyclina* limestone and marl. The bryozoan marl is up to 20 m thick. The topmost part of the succession is *Globigerina* marl (KÁZMÉR et al., 1993).

There is an exception to the rule in borehole Helmberg 1. The succession starts with a biostrome of larger foraminifers intercalated with build-ups of corallinacean algae. Their total thickness is up to 25 m. There is about 6 m of bryozoan marl, topped by algal bioherm (RASSER et al., 2000).

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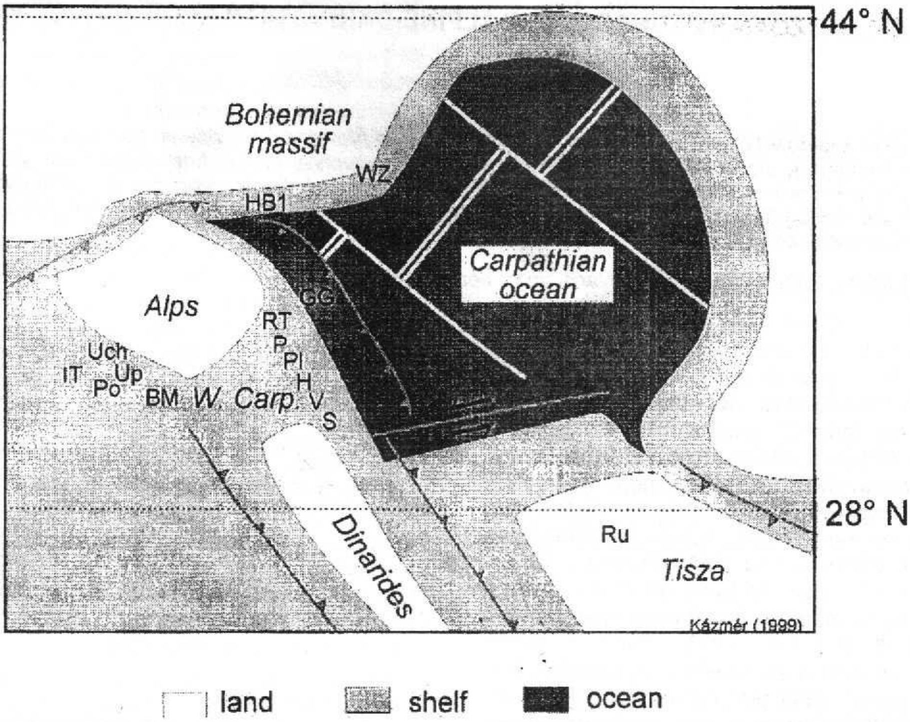

Figure 1 - Late Eocene bryozoan faunas within the Eocene palaeogeographic pattern of the Alpine-Carpathian region. Localities: H = Hybica (Slovakia); S = Štrba (Slovakia); HB1 = Helmberg 1 (Austria); BM = Buda Marl (localities: Mátyáshegy, western and eastern quarries, Ürom: Hungary); IT = Italy (Brendola, Pannone and Brentonico); Ru = Romania (localities around Cluj-Napoca); RT = Rajecké Teplice (Slovakia); P = Poluvsie; WZ = Waschberg Zone (localities Reingruberhöhe, Haselbach, Haidhof: Austria); Up = Úrhida-pit (Hungary); Pl = Partizánska Ľupča; V = Východná (Slovakia); GG = Gschliefgraben bei Gmunden (Austria); Uch = Úrhida-church (Hungary); Po = Possagno (Italy)

Bioclastic marl with larger foraminifers and corallinacean algae

While bryozoan zoaria are still common in this lithology, larger foraminifers and fragments of corallinacean algae dominate bioclasts. There is a higher diversity of encrusting bryozoans at these localities. Free-living bryozoans are common and *Lacrimula perfecta* is present. This species lives in less than 50 m depth (BRAGA & BARBIN, 1989) and its presence or absence can be used as palaeodepth indicator.

Localities:

- Úrhida-church, Hungary (ZÁGORŠEK & KÁZMÉR, in press)
- Partizánska Ľupča and Východná, Liptov basin, Slovakia (ZÁGORŠEK, 1992, 1994, 1997)
- Possagno, Italy (BRAGA, 1980)
- Gschliefgraben, Gmunden, Austria (ZÁGORŠEK, in press)
- Reingruberhöhe, Bruderndorf, Waschberg zone, Austria (ZÁGORŠEK, in press)

At Reingruberhöhe the lithology is dominated by corallinacean algae rather than by larger foraminifers.

Calcareous sandstone

Localities:

- Reingruberhöhe and in other localities of the Waschberg zone, Austria (ZÁGORŠEK, in press)
- Rajecké Teplice and Poluvsie, Western Carpathians, Slovakia (ZÁGORŠEK, 1992, 1994, 1997)
- Úrhida-pit, Hungary (ZÁGORŠEK & KÁZMÉR, in press)

Localities and faunas

Austria

Sediments of borehole *Helmberg 1* (32 km NE from Salzburg) were described by RASSER et al. (2000). The borehole penetrates the sedimentary cover of the Bohemian Massif in the foreland of the Alpine collisional belt. The Eocene bryozoan marl belongs to the Molasse (MALZER et al., 1993).

The borehole penetrated subhorizontal Eocene bryozoan marl (333-335 m). Besides a rich bryozoan fauna the marl contains only a few fragments of echinoids and shells of the brachiopod *Argyrotheca.* Altogether 109 species were determined. Most of them are of erect zoarial growth form, while a few are encrusting. Free-living and other growth forms are very rare.

The Waschberg zone localities (Reingruberhöhe, Haselbach, and Haidhof) are ca. 20 km NW from Vienna. The Waschberg zone is the sedimentary cover of the Bohemian Massif, sheared off its basement and folded during the Alpine orogeny in the Miocene (FUCHS, 1980). The best locality is an abandoned quarry at *Reingruberhöhe* near Bruderndorf (8 km NE of Stockerau). The quarry exposes a limonite-rich, reddish calcareous sandstone. It is rich in bryozoans and corallinacean algae. There are also larger foraminifers, mollusc fragments, echinoids, and small fish teeth (SEIFERT, 1980, 1982). Further localities (Haselbach, Haidhof) yielded only a few additional species.

We have only old specimens from Gschliefgraben bei Gmunden. Since new sampling is not possible at the moment, the locality being overgrown by bush, we omitted its study.

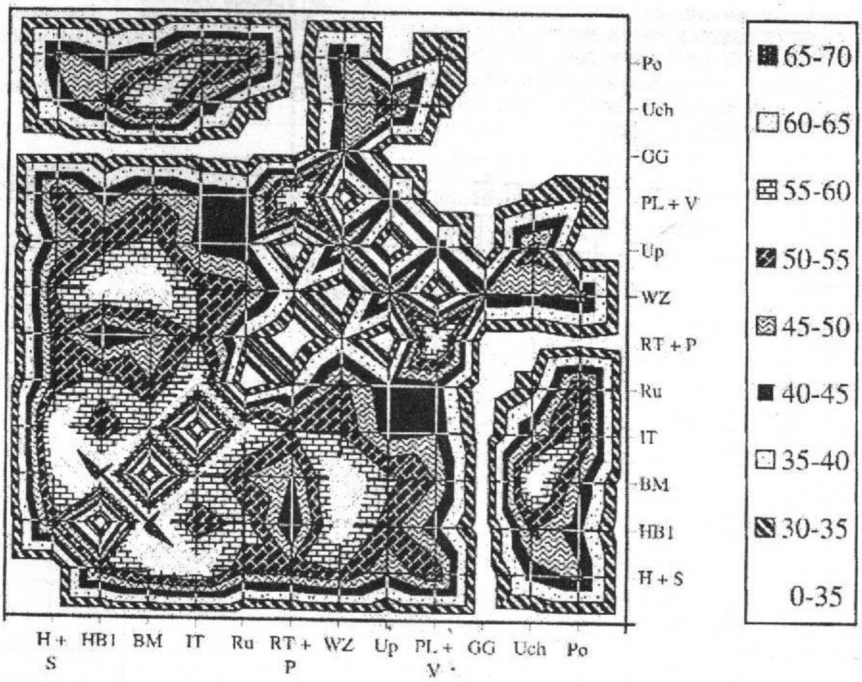

Figure 2 - Comparison chart of localities. Numbers are Kojumdgieva similarity coefficients. (Abbreviations see Fig. 1)

Italy

The localities Brendola, Possagno, Pannone, and Brentonico (BRAGA, 1963, 1965, 1980) are at the margins of the Lessini shelf of the Southern Alps (BOSELLINI, 1989). The shelf was the flexural bulge of the Paleogene Dinaric overthrusts (DOGLIONI & BOSELLINI, 1987).

Hungary

The Hungarian Paleogene basin (BÁLDI-BEKE & BÁLDI, 1991) is a retroarc basin of the Eocene Carpathian orogen (TARI et al., 1993). Before the Miocene it has been adjacent to the Southern Alps (KÁZMÉR & KOVÁCS, 1985).

One hundred and thirty bryozoan species have been described from six localities in the Transdanubian Central Range (ZÁGORŠEK & KÁZMÉR, in press). The localities are Mátyáshegy western and eastern quarry in Budapest, and Üröm and Úrhida villages. Erect rigid growth forms dominate the associations. At Úrhida a number of free-living species were found.

Slovakia

The localities Hybica, Štrba, Rajecké Teplice, Poluvsie, Partizánska Ľupča and Východná are along the northern margin of the Central West Carpathians (GROSS & KÖHLER, 1980), the forearc basin of the Carpathian orogen (TARI et al., 1993). Altogether 106 species were found (ZÁGORŠEK, 1992, 1994, 1997), mostly of erect growth form.

Romania

The Transylvanian Basin, a Paleogene forearc basin (PROUST & HOSU, 1996) hosts an impressive succession of terrestrial to shallow marine sediments (POPESCU, 1984). The bryozoan marl, described by KOCH (1894) has a rich fauna (PERGENS, 1887). Ghiurca (1981, 1987) briefly discussed the localities around Cluj-Napoca, and the species were listed, unfortunately without any description or illustration. The lists contain many synonyms and disused names. A revision was attempted but failed due to the lack of ample descriptions.

BIOGEOGRAPHY

Altogether 239 Late Eocene bryozoan species were found, described or mentioned from 12 localities in the Alpine-Carpathian region. Twenty-four of them occur in more than eight localities (Table 2).

The most common species is *Alderina subtilimargo* (REUSS, 1864) (Pl. I, fig. 1), which occurs in all studied localities. Both *Mecynoecia proboscidea* (MILNE EDWARDS, 1838) (Pl. I, fig. 3) and *Onychocella subpyriformis* (D'ARCHIAC, 1846) (Pl. I, fig. 2) occur in 11 localities.

Faunas were compared by the Kojumdgieva similarity coefficient (BRAGA et al., 1996).

$$K = (Ca\% + Cb\%)/2$$

where

$Ca\% = C/A.\ 100$

$Cb\% = C/B.\ 100$

where

A = number of species from locality a

B = number of species from locality b

C = number of species common both to a and b

Table 3 and Fig. 2 display the results. If the Kojumdgieva similarity coefficient is higher than 50, the faunas are considered very similar.

The two most similar localities are Mátyáshegy at Budapest and Helmberg 1 at Salzburg (K = 66.4). These two localities have 158 species in total and 78 of them occur at both. The host rock is bryozoan marl. Further very similar localities are the ones in the Waschberg zone, Austria, where the sediment is calcareous sandstone.

Table 1 - A complete list of found, described or mentioned Late Eocene bryozoan species from the Alpine-Carpathian region: H = Hybica (Slovakia); S = Štrba (Slovakia); HB1 = Helmberg 1 (Austria); BM = Buda Marl (localities: Mátyáshegy, western and eastern quarries, Ürom: Hungary); IT = Italy (Brendola, Pannone and Brentonico); Ru = Romania (localities around Cluj-Napoca); RT = Rajecké Teplice (Slovakia); P = Poluvsie; WZ = Waschberg Zone (localities Reingruberhöhe, Haselbach, Haidhof: Austria); Up = Úrhida-pit (Hungary); Pl = Partizánska Ľupča; V = Východná (Slovakia); GG = Gschliefgraben bei Gmunden (Austria); Uch = Úrhida-church (Hungary); Po = Possagno (Italy)

TAXA	Bryozoan marl					Calcareous sandstone			Bioclastical marl			
	H+S	HB1	BM	IT	Ru	RT+P	WZ	Up	Pl+V	GG	Uch	Po
"Chaperia" spinella Zagorsek	*		*					*	*			
"Puellina" chelys (Koschinsky)		*	*	*	*						*	
"Puellina" pupula (Reuss)		*	*				*					
"Schizoporella" fissimargo (Reuss)			*									
"Schizoporella" scrobiculata (Reuss)	*	*	*	*	*				*		*	
"Tetraplaria" schreibersi (Reuss)	*	*	*	*	*		*					
Adeonella minor (Reuss)	*	*	*	*	*		*			*	*	*
Adeonella ornatissima (Stoliczka)		*					*					
Adeonellopsis sp.n. 1							*					
Adeonellopsis sp.n. 2		*	*				*					
Adeonellopsis coscinophora (Reuss)	*		*	*			*					
Adeonellopsis porina (Romer)	*	*	*	*	*		*				*	*
Adeonellopsis subquadrangularis (Reuss)		*					*					
Aimulosia manzonii (Neviani)					*		*					
Alderina subtilimargo (Reuss)	*	*	*	*	*	*	*	*	*	*	*	*
Amphiblestrum appendiculata (Reuss)	*	*	*	*	*		*		*			*
Anornithopora pretiosa (Reuss)	*											
Arthropoma rugulosa (Reuss)		*					*					
Arthropoma sparsipora (Reuss)	*		*	*			*				*	
Bactridium hagenowi Reuss	*	*	*	*	*		*	*				
Batopora multiradiata Reuss		*	*	*	*		*		*		*	*
Batopora rosula (Reuss)				*	*							*
Batopora scrobiculata Koschinsky		*	*	*	*							
Berenicea rotula (Reuss)		*										
Biflustra clathrata (Philippi)			*								*	
Biflustra texturata (Reuss)		*	*	*	*		*	*	*		*	
Biretopora disticha Goldfuss					*							
Bobiesipora fasciculata (Reuss)		*	*				*	*			*	
Buffonellodes rhomboidalis (Canu & Bassler)	*											
Caberoides canaliculata Canu	*		*									
Caberoides grignonensis Canu			*	*								
Callopora dumerilii (Savigny-Audouin)							*			*		
Calpensia gracilis (Munster)			*	*		*	*		*			
Calpensia nobilis (Esper)				*	*							
Calpensia polysticha (Reuss)	*		*	*	*	*			*			
Castanopora calomorpha (Reuss)		*	*									
Cellaria reussi d'Orbigny	*	*	*	*	*		*					
Cellepora angistoma (Reuss, 1869)					*							
Cellepora conglomerata Goldfuss	*			*	*							
Cellepora diplostoma Reuss				*								
Celleporaria globularis (Bronn)		*	*	*	*		*	*		*	*	
Ceriopora depressa (Reuss)					*							
Cheilonella prominens Reuss		*										
Cheilopora orbifera Canu & Bassler		*	*									
Chlidoniopsis sp. n.							*					
Chlidoniopsis vindobonensis (Reuss)	*		*	*			*					
Conopeum hookeri (Haime)	*				*							

Table 1 (continued)

TAXA	Bryozoan marl					Calcareous sandstone			Bioclastical marl			
	H+S	HB1	BM	IT	Ru	RT+P	WZ	Up	Pl+V	GG	Uch	Po
Costaticella sp. n. 1							*					
Costaticella sp. n. 2							*					
Crassimarginatella macrostoma (Reuss)	*	*	*	*	*	*	*	*	*		*	
Crisia eburnea (Linnaeus)		*	*		*		*					
Crisia elongata Milne Edwards	*	*	*	*			*					*
Crisia haueri Reuss			*	*								*
Crisia hoernesii Reuss	*	*	*	*	*		*			*		*
Crisia strangulata Buge, 1957					*							
Crisia subaequalis Reuss	*			*								
Cyclicopora laticella Canu & Bassler	*		*				*				*	
Cyphonella nodosa Koschinsky		*						*				
Decurella toarensis Mongereau & Braga				*								
Desmeplagioecia tenuis (Reuss)				*								*
Diastopora flabellum Reuss							*					
Diastopora nova Pergens & Meunier					*							
Diastopora sp.							*					
Diastopora sparsa (Reuss)		*			*							
Dicasignetella sp.							*					
Disporella coronula (Reuss)		*	*	*	*		*		*			*
Disporella grignonensis Milne Edwards	*	*	*		*	*	*		*			*
Disporella hispida (Fleming)					*							
Disporella radiata (Savigny-Audouin)	*	*	*		*		*					*
Ditaxipora internodia (Waters)		*										
Ditaxipora pannonensis Ant., B. & F.		*		*								
Ditaxiporina septentrionalis (Waters)		*	*	*			*					
Dittosaria prima (Reuss, 1866)					*							*
Entalophora geinitzi Reuss		*			*		*					
Escharella grotriani (Stoliczka)	*		*				*					*
Escharella tenera (Reuss)	*	*	*				*			*		
Escharella ventricosa (Hassall)		*										
Escharoides aliferus (Reuss)	*	*	*	*	*							
Escharoides coccinea (Abildgaard)	*		*	*	*		*					*
Escharoides crenilabris (Reuss)	*		*				*					
Escharoides mamillata (Wood)							*					
Exidmonea atlantica D., M. & P.	*	*	*	*	*		*	*	*		*	
Exidmonea concava (Reuss)				*	*							*
Exidmonea crisiiforma Zagorsek	*											
Exidmonea giebeli (Stoliczka)	*	*	*	*	*		*		*			
Exidmonea hoernesi (Stoliczka)	*	*	*	*	*	*	*		*			*
Exidmonea villaltae (Reguant)	*	*	*		*	*			*			
Exochella? labiosa (Reuss)			*	*								
Exochoecia compressa (Reuss)	*	*	*	*	*	*	*				*	
Fascigera dimidiata (Reuss)	*			*		*						*
Faveolaria sp.n.			*		*						*	
Fedora bidentata (Reuss)	*	*	*	*	*							
Filisparsa cuvillieri Debourle	*					*			*			
Filisparsa fallax Canu & Bassler	*			*								
Filisparsa orakeiensis Stoliczka	*			*			*					
Filisparsa tenella Stoliczka		*			*		*					
Gen. nov. 1 sp.n. 1		*					*					
Gen. nov. 1 sp.n. 2			*								*	

Table 1 (continued)

TAXA	Bryozoan marl					Calcareous sandstone			Bioclastical marl			
	H+S	HB1	BM	IT	Ru	RT+P	WZ	Up	Pl+V	GG	Uch	Po
Gen. nov. 2 sp.n.							*					
Gen. nov. 3 sp.n. 1			*									
Gen. nov. 3 sp.n. 2		*	*				*					
Gen. nov. 4 sp.n.			*									
Gen. nov. 5 sp.n.		*	*								*	
Gephyrotes convexa Canu & Bassler			*				*					
Gigantopora duplicata (Reuss)	*	*	*	*	*		*					*
Gigantopora lyratostoma (Reuss)	*	*	*	*	*		*					
Hemicyclicopora parajuncta Canu & Bassller							*					
Herentia hyndmanni (Johnston)		*	*				*					
Heteropora sp.							*			*		
Heteropora subreticulata Reuss	*	*	*	*	*	*	*		*			
Hippomenella bragai Zagorsek	*	*					*					
Hippomenella megalota Reuss							*					
Hippomenella transversora Canu & Bassler	*											
Hippomonavella exarata (Reuss)	*	*	*	*			*			*		
Hippomonavella imbricata (Reuss)		*										
Hippomonavella stenosticha (Reuss)	*		*	*			*				*	
Hippoporella pauper (Reuss)							*					
Hippoporina globulosa (d'Orbigny)		*										
Hippoporina pertusa (Esper)										*		
Hippoporina punctifera Canu	*								*			
Hippoporina rarepunctata (Reuss)		*										
Hornera asperula Reuss	*			*	*				*			
Hornera concatenata Reuss	*	*		*	*		*					*
Hornera frondiculata frondiculata Mong.	*	*	*	*	*	*	*				*	*
Hornera seriatopora Reuss	*					*			*			
Hornera simplicissima Braga & Barbin		*		*			*					
Hornera subannulata Philippi	*	*			*	*			*			*
Hornera verrucosa Reuss				*	*		*			*		
Houzeauina parallela (Reuss)			*	*		*	*		*			
Iodictyum sp.n.		*	*									
Iodictyum rubeschii (Reuss)			*				*					
Kionidella excelsa Koschinsky	*	*	*	*	*		*		*			*
Labioporella dartevellei Cheetham			*									
Lacrimula perfecta (Accordi)			*	*			*	*	*		*	*
Lagenipora ampullacea (Roemer)							*					
Lagenipora tuba (Manzoni)							*					
Lagenipora urceolaris Goldfuss							*					
Lunulites quadrata (Reuss)				*	*				*		*	*
Margaretta cereoides (Ellis & Solander)	*	*	*	*	*			*	*		*	*
Mecynoecia anomala (Reuss)							*			*		
Mecynoecia proboscidea (Milne Edwards)	*	*	*	*	*	*	*	*	*		*	*
Mecynoecia pulchella (Reuss)	*			*	*		*					*
Meniscopora syringopora (Reuss)	*	*	*	*			*				*	
Metradolium obliquum Canu & Bassler		*					*					
Metrarabdotos maleckii Cheetham	*	*			*		*				*	
Micropora sp.n.		*	*					*				
Micropora coricea Esper							*					
Micropora hexagona Zagorsek	*	*	*				*		*			

Table 1 (continued)

TAXA	Bryozoan marl					Calcareous sandstone			Bioclastical marl			
	H+S	HB1	BM	IT	Ru	RT+P	WZ	Up	Pl+V	GG	Uch	Po
Mollia patellaria (Moll)							*					
Monoporella venusta (Reuss)							*					
Nellia tenella Lamarck				*	*							*
Nematifera reticuloides Canu & Bassler	*								*			
Nematifera susannae Zágoršek	*	*	*			*			*		*	
Notoplites sp.			*									
Odontoporella sp.			*									
Ogivalina dimorpha (Canu)		*	*				*					
Oncousoecia biloba (Reuss)		*	*	*	*		*				*	*
Onychocella subpyriformis (d'Archiac)	*	*	*	*	*	*	*	*	*		*	*
Orbitulipora petiolus Lonsdale	*		*	*			*					
Parasmittina saccoi (Canu)		*	*									
Parasmittina telum (Canu & Bassler)			*									
Perigastrella granulata Zágoršek	*	*	*									
Perigastrella oscitans Canu & Bassler	*											
Phylactellipora tubiceps (Reuss)												*
Plagioecia cf. concreta Canu & Bassler			*								*	
Platonea pluma (Reuss)	*			*								
Pleuronea fenestrata (Busk)			*		*						*	
Pleuronea reticulata (Reuss)				*	*							
Polyascosoecia coronopus (Canu & Bassler)	*	*	*		*		*		*		*	
Porella clavula (Canu & Bassler		*	*	*	*		*					
Poricellaria complicata (Reuss, 1869)		*	*				*					*
Porina sp.n.		*	*									
Porina coronata (Reuss)	*	*	*	*	*		*	*			*	*
Porina duplicata (Reuss)			*	*			*					
Porina labrosa (Reuss)	*		*	*					*			
Prenantia phymatopora (Reuss)	*	*	*	*	*		*	*				
Puellina scripta (Reuss)	*											
Puellina (Cribrilaria) haueri (Reuss)		*	*	*	*						*	
Puellina (Cribrilaria) manzonii (Reuss)							*					
Puellina (Cribrilaria) radiata (Moll)	*	*	*	*	*		*					*
Pyriora huckei Buge							*					
Ramphonotus monopora (Reuss)	*			*		*			*			
Reteporella simplex (Busk)	*	*	*	*			*					
Reteporella subovata (Stoliczka)		*	*				*				*	
Reteporella tamaninii A., B & F.	*											
Reteporella tuberculata (Reuss)	*	*	*	*	*		*	*	*		*	
Reussia (Smittina) regularis (Reuss)	*	*	*	*			*					*
Rhamphostomella brendolensis Waters				*								*
Rosseliana rosselii (Audouin)	*	*	*	*			*				*	
Schizomavella larva (Reuss)			*	*	*		*					
Schizoporella bisulca (Reuss)	*			*	*							
Schizoporella dunkeri (Reuss)			*	*								
Schizoporella tetragona (Reuss)		*										
Schizosmittina sp.n.			*								*	
Scrupocellaria brendolensis Waters	*		*	*	*		*					*
Scrupocellaria gracilis Reuss				*	*		*					*
Scrupocellaria montecchiensis Waters	*			*								
Siphonicytara cf. excentrica Gordon & d'Ho							*					
Smittina cervicornis (Pallas)	*	*	*		*		*	*			*	

Table 1 (continued)

TAXA	Bryozoan marl					Calcareous sandstone			Bioclastical marl			
	H+S	HB1	BM	IT	Ru	RT+P	WZ	Up	Pl+V	GG	Uch	Po
Smittina porelloides Canu & Bassler			*									
Smittipora grandiconis Zagorsek									*	*		
Smittipora tenuis (Canu & Bassler)									*			
Smittistoma mortisaga (Stoliczka)												*
Smittoidea angulata (Bronn)			*									
Smittoidea circumornata (Reuss)			*									
Smittoidea excentrica (Reuss)		*	*		*		*					
Sparsiporina elegans (Reuss)	*	*	*	*			*		*			*
Spiropora verticillata Goldfuss		*			*							
Stamenocella midwayanica Canu & Bassler				*								
Steginoporella sp.n.		*					*					
Steginoporella cellariiformis Cheetham									*			
Steginoporella cucullata (Reuss)		*	*		*		*				*	
Steginoporella elegans chattiensis P.& D.		*	*		*		*					
Steginoporella firma (Reuss)	*			*			*					
Steginoporella haidingeri (Reuss)	*	*	*	*		*	*	*	*			
Steginoporella montenati David & Pouyet	*											
Stenosipora sp.n.			*									
Stenosipora protecta (Koschinsky)		*		*								
Stenosipora reussi (Stoliczka)		*	*	*							*	
Stenosipora simplex (Koschinsky)	*	*	*				*	*	*			
Stephanollona otophora (Reuss)		*	*									
Stomatopora cf. minima Roemer		*			*							
Stomatopora divaricata (Reuss)		*										
Tervia serrata (Reuss)	*	*	*	*	*		*	*			*	
Thalamoporella neogenica Buge			*									
Trochiliopora beyrichii (Reuss)	*	*	*		*	*	*		*			*
Tubucella mammillaris (Milne Edwards)	*	*	*				*	*			*	
Tubucella papillosa (Reuss)	*	*	*	*	*		*				*	*
Tubulipora congesta Reuss							*			*		
Tubulipora disticha (Michelin)					*							
Tubulipora flabellaris (Fabricius)					*						*	*
Tubulipora serpens (Linne)					*							
Umbonula macrocheila (Reuss)					*		*					
Umbunula monoceros (Reuss)			*				*					
Unifissurinella boulangeri Poignant		*					*					
Vibracella trapezoidea (Reuss)	*		*	*	*		*	*	*		*	*
Vincularia fragilis Defrance	*			*								
Vincularia subsymmetrica (Canu)				*	*		*					
Ybselosoecia typica (Manzoni)				*	*							
Total number of taxa 239	95	110	126	100	91	21	127	23	43	13	46	46

The bioclastic marl and calcareous sandstone localities seem to be less prone to long-distance similarity. Being shallower marine than the bryozoan marl, the composition of these associations is more sensitive to the local environment. Similarity indices suggest that associations in nearby localities are more similar than in far-away localities. Therefore localities Rajecké Teplice and Poluvsie are more similar to nearby Partizánska Ľupča and Východná (as well as to Hybica and Štrba) than to Úrhida-pit or to the Waschberg Zone.

Similarity indices between bioclastic marl localities have their lowest values; possibly this lithology is heterogeneous - and also the diversity is the lowest.

DISCUSSION

Bryozoan radiation had a peak in the Eocene (TAYLOR & LARWOOD, 1990), as spectacularly illustrated by the large number of high-diversity faunas in the Alpine-Carpathian region. The region went through significant tectonic deformation and displacement of terranes since the deposition of the bryozoan-containing sediments in Late Eocene time (KÁZMÉR & KOVÁCS, 1985; CSONTOS, 1995). A palaeogeographic map (Fig. 1A), based on the reconstruction of palaeolatitudinal history of the displaced terranes (MÁRTON, 1993; KÁZMÉR et al., 1999) illustrates the Priabonian position of the bryozoan faunas. Kojumdgieva indices added to the map (Fig. 1B) suggest that similarity of the faunas is independent of their distance, and is probably determined by regional environmental conditions rather than by large-scale dispersal history.

Faunas hosted by bryozoan marl, the most deep-water sediment among the studied ones, are highly similar, despite their position on widely displaced terranes and in different geodynamic setting (both in foreland, forearc, and retroarc basins). The dispersal of deep-water bryozoan faunas was unlimited, i.e. not disturbed by any geographic barrier, although their lecitotrophic larvae cannot survive long-distance planktonic transport (BRAGA, 1987). The appearance of deep-water faunas in successions of continental shelves has been explained by upwelling of cold water in a time of global climate deterioration (ZÁGORŠEK, 1996) and/or by filling the ecological niches of decimated larger foraminifer faunas on the same shelves (KÁZMÉR, 1999).

Table 2 - Bryozoan species occurring in more than eight localities in the Alpine-Carpathian region.

TAXA	number of localities
Alderina subtilimargo (Reuss)	12
Mecynoecia proboscidea (Milne Edwards)	11
Onychocella subpyriformis (d'Archiac)	11
Crassimarginatella macrostoma (Reuss)	10
Adeonella minor (Reuss)	9
Eximdmonea hoernesi (Stoliczka)	9
Eximdmonea atlantica D., M. & P.	9
Hornera frondiculata frondiculata Mong.	9
Vibracella trapezoidea (Reuss)	9
Margaretta ceroides (Ellis-Solander)	9
Porina coronata (Reuss)	9
Reteporella tuberculata (Reuss)	9
Adeonellopsis porina (Romer)	8
Kionidella excelsa Koschinsky	8
Batopora multiradiata Reuss	8
Biflustra savartii texturata (Reuss)	8
Celleporaria globularis (Bronn)	8
Crisia hoernesii Reuss	8
Exochoecia compressa (Reuss)	8
Heteropora subreticulata Reuss	8
Steginoporella haidingeri (Reuss)	8
Tervia serrata (Reuss)	8
Trochiliopora beyrichii (Reuss)	8
Tubucella papillosa (Reuss)	8

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Table 3 - Kojumdgieva similarity indices (Braga et al., 1996) for Late Eocene bryozoan faunas in the Alpine-Carpathian region.

	H + S	HB1	BM	IT	Ru	RT + P	WZ	Up	PL + V	GG	Uch	Po
H + S		52,9	60	63,6	51,6	52,3	55,2	45,9	54,1	21,8	42	46,8
HB1	52,9		66,4	50,6	57,3	39,7	62,7	52,6	42,1	25,8	50,8	41,6
BM	60	66,4		60,1	50,2	44,5	64,1	56,6	50	25,5	63,8	46
IT	63,6	50,6	60,1		61,9	54,7	54,5	42,7	44,9	26,1	46	57,1
Ru	51,6	57,3	50,2	61,9		35,2	51,8	40,9	42,8	22	32,7	55,6
RT + P	52,3	39,7	44,5	54,7	35,2		36,1	18,2	63,8	6,2	24,3	27,7
WZ	55,2	62,7	64,1	54,5	51,8	36,1		48,6	26,4	46,5	44,5	47,4
Up	45,9	52,6	56,6	42,7	40,9	18,2	48,6		43,4	12	52,2	22,8
PL + V	54,1	42,1	50	44,9	42,8	63,8	26,4	43,4		10	31,5	36
GG	21,8	25,8	25,5	26,1	22	6,2	46,5	12	10		14,8	9,9
Uch	42	50,8	63,8	46	32,7	24,3	44,5	52,2	31,5	14,8		28,3
Po	46,8	41,6	46	57,1	55,6	27,7	47,4	22,8	36	9,9	28,3	

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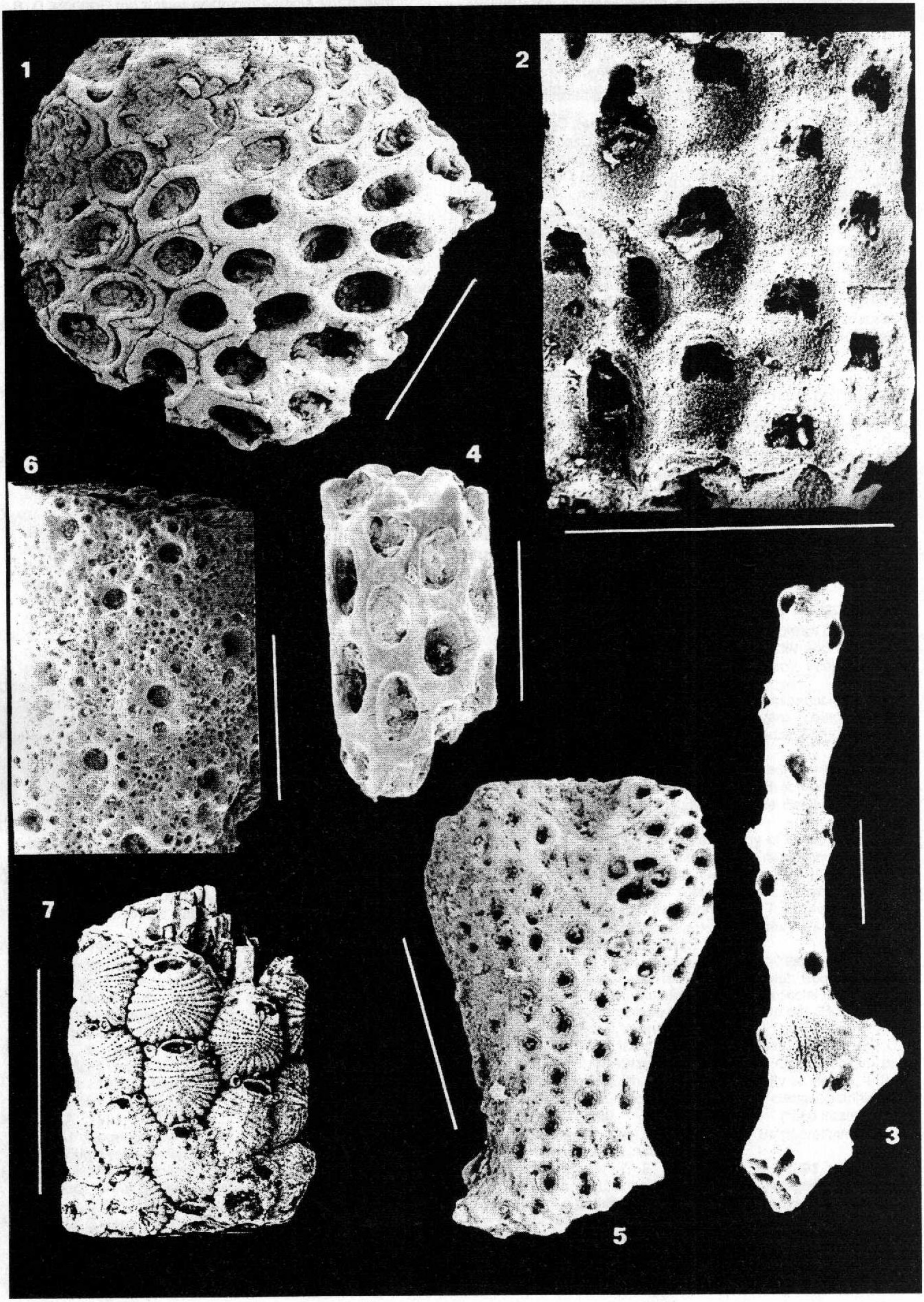
Plate I - The most frequent Late Eocene bryozoan species of the Alpine-Carpathian region.

Fig. 1. *Alderina subtilimargo* (REUSS). Helmberg 1 borehole (sample 2336-1)
Fig. 2. *Onychocella subpyriformis* (D'ARCHIAC). Hybica.
Fig. 3. *Mecynoecia proboscidea* (MILNE EDWARDS). Reingruberhöhe.
Fig. 4. *Crassimarginatella macrostoma* (REUSS). Reingruberhöhe.
Fig. 5. *Hornera frondiculata frondiculata* MONGEREAU. Haidhof.
Fig. 6. *Porina coronata* (REUSS). Mátyáshegy, western quarry.
Fig. 7. Cribrilinidae - *Castanopora calomorpha* (REUSS). Mátyáshegy, western quarry.

All scale bars are 1 mm.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