Mosaic of environments recorded by bryozoan faunas from the Middle Miocene of Hungary

Pierre Moissette [a,*], Alfréd Dulai [b], Gilles Escarguel [a],
Miklós Kázmér [c], Pál Müller [d], Jean-Paul Saint Martin [e]

[a] UMR 5125 PEPS CNRS; Université Lyon I, Campus de la Doua, 69622 Villeurbanne cedex, France
[b] Department of Geology and Palaeontology, Hungarian Natural History Museum, H-1431 Budapest, P.O. Box 137, Hungary
[c] Department of Palaeontology, Eötvös University, H-1518 Budapest, P.O. Box 120, Hungary
[d] Hungarian Geological Institute, H-1143 Budapest, Stefánia út 14, Hungary
[e] UMR 5143 CNRS, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France

Abstract

The marine sediments of the Badenian (Middle Miocene) of Hungary (Pannonian Basin, Central Paratethys) are composed of abundant bryozoan skeletal grains. Seventy-one bulk samples collected at 18 localities (outcrops and boreholes) yielded a total number of 238 bryozoan species.

In order to reconstruct the Badenian palaeoenvironments, the present study investigates the composition of this very diverse fauna using a combination of statistical and palaeoecological methods. The statistical analyses make use of Cluster Analysis and Non-metric Multi-Dimensional Scaling. The palaeoecological approaches are based on the known ecological requirements of the bryozoan colonial growth forms and of the numerous extant species.

Five facies have first been differentiated on the basis of sedimentological and palaeontological features: coral buildups, coralline algal limestones, biocalcarenites, sands, and marls. Each of them is characterized by the abundance, the diversity and the types of growth forms of the bryozoans.

The palaeoecological, statistical and facies analyses further permitted to identify four depositional settings: carbonate platform (distal and proximal), terrigenous platform, slope, and basin. These environments developed at depths between 0 to about 300 m in a mixed carbonate–siliciclastic depositional system. Skeletal production and spatial distribution of carbonate factories were predominantly controlled by terrigenous input. This resulted in a complex mosaic of facies/habitats where rich bryozoan faunas could thrive.

Many warm-water organisms, among them foraminifers, zooxanthellate corals, molluscs, bryozoans, and echinoids, were recorded from the study sites. The coexistence of coralgal and bryomol carbonate skeletal assemblages in this subtropical setting is explained mostly by variations in the productivity of surface waters. Periods of nutrient enrichment and increased benthic eutrophication affected coral diversity and abundance in favour of bryozoans.
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* Corresponding author. Tel.: +33 472 43 11 65; fax: +33 472 44 83 82.
E-mail addresses: Pierre.Moissette@univ-lyon1.fr (P. Moissette), dulai@nhmus.hu (A. Dulai), Gilles.Escarguel@univ-lyon1.fr (G. Escarguel), kazmer@ludens.elte.hu (M. Kázmér), mullerp@mafi.hu (P. Müller), jpsmart@mnhn.fr (J.-P. Saint Martin).

1. Introduction

The Paratethys was an epicontinental sea (Fig. 1) that developed as a relict of the ancient Tethys Ocean and existed between the end of the Eocene and the Middle Miocene. It consisted of a series of basins, which were intermittently connected to the Mediterranean and the Indo-Pacific (Rögl and Steininger, 1983; Rögl, 1998, 1999; Meulenkamp and Sissingh, 2003). The area from the present-day Austria to Poland and Romania is called the Central Paratethys (Fig. 2). The Badenian is a regional stage used in the Central Paratethys (Papp et al., 1978; Nagymarosy and Müller, 1988) for part of the Middle Miocene (Langhian to Middle Serravallian).

Thick marine deposits accumulated during the Badenian in the whole Central Paratethys and particularly in its central and largest part, the Pannonian Basin, where Hungary is situated (Bérczi et al., 1988; Royden and Báldi, 1988; Royden and Horváth, 1988; Hámor, 1995; Vakarcs et al., 1998). Abundant and diverse communities of organisms, above all coralline algae and invertebrates, are often associated with these sediments.

The Badenian bryozoans of Hungary have been little studied. As revealed by a previous paper (Moissette et al., 2006), they are however abundant and diverse in various marine facies: biogenic limestones (coralline algae and corals), biocalcarenites, sands and sandstones, and marls. The material collected at 18 localities (outcrops and cores) yielded a total of 238 species: 176 cheilostomes, 59 cyclostomes, and 3 (boring) ctenostomes.

Bryozoans have been shown to be useful tools for palaeoenvironmental reconstructions (Stach, 1936; Lagaaij and Gautier, 1965; Labracherie, 1973; Pedley, 1976; Harmelin, 1988; Smith, 1995; Hageman et al., 1997; Moissette, 2000; Amini et al., 2004). Two methods are generally used for the palaeoecological analysis of Tertiary faunas: an actualistic approach based on the known ecology of extant species, and analysis of colonial morphotypes. In addition, we perform here statistical multivariate analyses to investigate the inter-assemblage resemblances on the single basis of their compositional similarities.

The main purpose of the present study is to reconstruct the palaeoenvironments of the Pannonian Basin during the Badenian. Another objective of this paper is to examine why deposits considered as indicative of warm climate (coralgal skeletal assemblage) could coexist with typical cool-water heterozoan assemblages of abundant bryozoans and molluscs (bryomol).

2. Geological setting

The Badenian sedimentation of the Central Paratethys is of a mixed siliciclastic–carbonate type. A relatively high terrigenous clastic influx came from the uplifting Alpine chains around the basin. On the other hand, platforms and other shallow areas, placed distally or isolated from areas with siliciclastic input were characterized by limestone formation. These limestones were originally described in the Vienna Basin and designated as Leithakalk or Leitha limestone (Friebe, 1988, 1993;
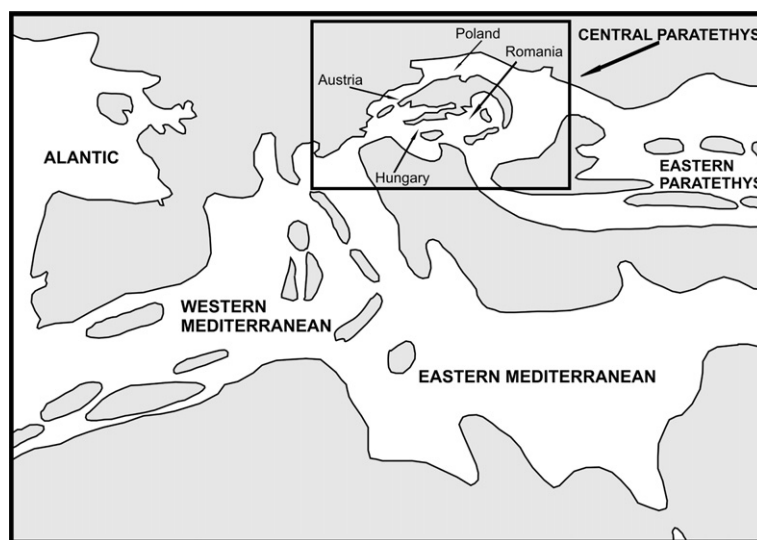

Fig. 1. Palaeogeographic sketch map of southern Europe and northern Africa during the largest extension of the Paratethys in Early Badenian time (modified from Alvinerie et al., 1992; Rögl, 1998; Meulenkamp and Sissingh, 2003; Popov et al., 2004).
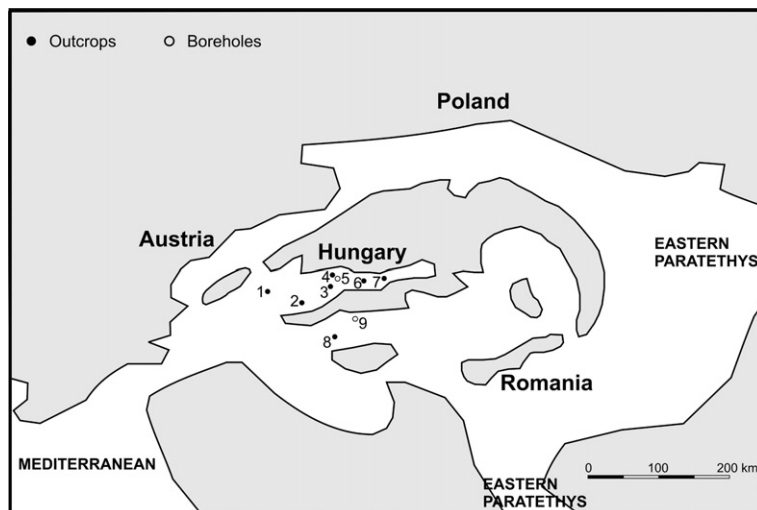
Fig. 2. Palaeogeographic sketch map of the Central Paratethys (modified from Rögl, 1998). Numbers correspond to studied localities or groups of localities and cores: 1. Fertőrákos (= Kroisbach *in* Canu and Bassler, 1925); 2. Várpalota; 3. Budapest (Diósd, Rákos, Őrsvezér tere); 4. Börzsöny Mountains (Visegrád, Zebegény, Nagymaros–Törökmező, Szob, Kemence); 5. Szokolya-2; 6. Cserhát Mountains (Mátraverebély = "Szentkút", Sámsonháza, Mátraszőllős); 7. Borsodbóta; 8. Mecsek Mountains (Kishajmás, Kovácsszénájai lake); 9. Tengelic-2.

Pisera, 1996; Riegl and Piller, 2000). In Hungary, its various facies were later subdivided into different formations: Rákos, Sámsonháza, Ebes, Abony, Pécsszabolcs (Császár, 1997). Most of the Badenian limestones, rich in coralline red algae, vary in texture from grainstone to wackestone and in some areas these deposits are intercalated with small coral buildups (Müller, 1984; Pisera, 1996; Randazzo et al., 1999; Riegl and Piller, 2000; Saint Martin et al., 2000; Górka, 2002). Consequently, the original term Leithakalk (Lajtamészkő in Hungarian) still has an extended use and seems to be more practical than the use of the five formation names. Deeper water sediments (marls and silts) are widespread in basinal settings. In some cases the deeper water marls are intercalated with grainstone lenses resulting from gravitational redeposition of platform deposits into neighbouring basins (Schmid et al., 2001).

The shallow-water deposits of the Paratethys, predominantly limestones and sandstones, are generally devoid of any planktonic fossils, thus their age is extremely difficult to determine (Senes, 1975; Papp et al., 1978; Nagymarosy and Müller, 1988; Vakarcs et al., 1998). A simple bipartitional subdivision of the Badenian stage (Early and Late) is consequently used in this paper (Moissette et al., 2006).

The bryozoan faunas under study are always accompanied by more or less numerous skeletal remains belonging to other groups of organisms: coralline algae, foraminifers, calcareous and siliceous sponges, scleractinian corals, serpulid worms, bivalves, gastropods, scaphopods, polyplacophorans, brachiopods, crabs, ostracods, barnacles, echinoids, crinoids, and fishes.

Calcareous fragments and whole organisms thus constitute the bulk of most of the studied sediments. Volcanic products (micas, quartz, pumice) are abundant in all samples, excepted in those collected from the Tengelic-2 borehole. Terrigenous components (quartz, silt and clay minerals) also occur in practically all samples.

The relatively high biodiversity observed is partly the result of the availability of various types of habitats: algal crusts and rhodoliths, skeletal macrofaunas, rocky and soft bottoms at various depths, and possibly seagrasses and seaweeds. Most bryozoan colonial morphotypes/ species need to attach themselves to a hard (or more rarely firm but flexible) substratum. This is reflected in the Badenian of Hungary by numerous colonies found on various types of substrates such as gravels and skeletal remains (mostly mollusc shells and other bryozoans, but often corals and red algae too). Nodular bryozoans frequently show a hole, more or less flattened, in the centre of their colonies; this indicates the presence of ephemeral unfossilized flexible substrates such as gorgonians, seagrasses or seaweeds, on which these bryozoans were attached during their life (Radócz, 1972; Bałuk and Radwanski, 1977; Hoffman, 1979).

Although the exact age of some of the deposits remains a matter of controversy, the following age assignments have been adopted. Most localities (Fig. 2) are considered as Early Badenian in age, whereas only

four outcrop localities and one borehole are attributed to the Late Badenian (Table 1).

3. Study material

3.1. Field material

Most of the material used in this study (43 samples taken from 16 sections or isolated outcrops: Fig. 2) was collected by the authors. Hungary is essentially a flat country and the main difficulty was finding sufficient adequate outcrops: steep hill flanks, quarries, road or railway cuts, etc. A weight of about 500 g was generally taken from loose sediments (marls, sands) and several kilograms from indurated or semi-indurated rocks (limestones, sandstones).

3.2. Core material

The Hungarian Geological Survey undertook in the 1950s and 1960s a great effort of coring. We were able to sample the Badenian interval of two cores made in predominantly argillaceous sediment: Tengelic-2 and Szokolya-2 (Fig. 2). These boreholes yielded only a few bryozoan fragments and species in respectively 8 and 20 samples. For the palaeoecological and statistical analyses, the levels from the same borehole and their rare

species, with their similar faunal and lithological attributes, were lumped together into a single sample.

3.3. Preparation of the samples

In the laboratory, sediment samples were treated with dilute hydrogen peroxide and then washed over a column of 6 sieves of diminishing mesh sizes: 2, 1, 0.5, 0.25, 0.125, and 0.063 mm. No bryozoan fragments were however found in the finer fraction and only very rare specimens occurred in the 0.125 mm fraction. Indurated or semi-indurated rocks were treated much the same way, but also broken into smaller pieces and brushed in order to detach fragments from the matrix. The dried residues were afterwards studied under a stereomicroscope to identify the species present and count the number of colonies or fragments.

4. Methods

Two palaeontological methods are used in this paper to reconstruct the Badenian environments. They are based on the known ecological requirements of the bryozoan colonial growth forms and of the numerous extant species. Complementary to this actualistic approach of palaeoenvironmental reconstruction, we performed multivariate ordination and clustering analyses of

Table 1
Main facies type, number of samples and age assignment for each studied locality

Locality	Facies	Number of samples	Age
Borsodbóta	Bioclastic gravely sand	3	Early Badenian
Kemence	Biocalcarenite	3	Early Badenian
Kishajmás	Algal limestone	2 (Mecsek1-2)	Early Badenian
Kovácsszénájai lake	Algal limestone	1 (Mecsek3)	Early Badenian
Mátraszőllős	Biocalcarenite	3 (Cserhát2-4)	Early Badenian
Mátraverebély	Biocalcarenite	4 (Cserhát5-8)	Early Badenian
Sámsonháza	Biocalcarenite	1 (Cserhát10)	Early Badenian
Szob	Argillaceous sand	3	Early Badenian
Szokolya-2 borehole	Sandy marl	20	Early Badenian
Törökmező (Nagymaros)	Algal limestone	1	Early Badenian
Várpalota	Mollusc-rich sand	3	Early Badenian
Visegrád	Biocalcarenite	1 (Visegrád1)	Early Badenian
Visegrád	Algal limestone	1 (Visegrád2)	Early Badenian
Visegrád	Coral Patch reef	1 (Visegrád3)	Early Badenian
Zebegény	Algal limestone	3	Early Badenian
Diósd	Coral patch reef	1 (Diósd1)	Late Badenian
Diósd	Biocalcarenite	1 (Diósd2)	Late Badenian
Fertőrákos	Biocalcarenite	1	Late Badenian
Őrsvezér tere (Budapest)	Bioclastic sand	4 (Őrsvezér tere1-4)	Late Badenian
Őrsvezér tere (Budapest)	Biocalcarenite	1 (Őrsvezér tere5)	Late Badenian
Rákos (Budapest)	Coral Patch reef	1 (Rákos1)	Late Badenian
Rákos (Budapest)	Sandy algal limestone	4 (Rákos2-5)	Late Badenian
Tengelic-2 borehole	Marl	8	Late Badenian

the occurrence and abundance data in order to explore and visualize the compositional similarities between samples and between localities.

4.1. Bryozoan colonial growth forms

Bryozoan colonies occur under several colonial morphotypes, called zoarial forms. Their growth has been correlated with various factors of the environment such as water depth, substrate type, water energy, and sedimentation rate (Stach, 1936, 1937; Lagaaij and Gautier, 1965; Schopf, 1969; Harmelin, 1988; McKinney and Jackson, 1989; Smith, 1995; Amini et al., 2004; Taylor et al., 2004). Since no zoarial form is restricted to a single habitat, it is the association and relative abundance of various colonial morphotypes that is above all useful for palaeoenvironmental interpretations (Harmelin, 1988; Nelson et al., 1988a; Smith, 1995; Hageman et al., 1997, 1998; Moissette, 2000; Amini et al., 2004).

Nine distinct zoarial forms are represented in the Badenian of Hungary (Fig. 3). Rare boring ctenostome species also occur in mollusc shells: *Orbignyopora archiaci*, *Spathipora* sp., and *Terebripora* sp. Most bryozoan species grow under only one zoarial form, but some plastic species are represented in the studied facies by two different morphotypes; they will be listed in the table corresponding to each zoarial form (Tables 2–6).

4.1.1. Membraniporiform

The colonies of this zoarial form are unilaminar and encrust mostly hard substrates. This morphotype is considered as characteristic of shallow depths, moderate to high water energy and relatively slow sedimentation rates.

The vast majority of the Hungarian Badenian species (149) belong to this zoarial form (Table 2). They are especially diverse in the algal and biocalcarenitic levels. Individually, none of these species is however abundant in the studied assemblages. Because of their colonial plasticity, four of these encrusting species may also occur under an erect bilaminar form: *Buffonellaria divergens*, *Emballotheca longidens*, *Tremopora radicifera*, and *Umbonula macrocheila*.

4.1.2. Celleporiform

In this kind of colony, the zooids are piled up without order in successive layers on various types of substrates. They constitute nodular massive or branching multilaminar colonies. This zoarial form also indicates shallow depths, with an optimum around −30 m (Spjeldnaes and Moissette, 1997; Moissette, 2000).

Among the 21 species belonging to this morphotype (Table 3) three are particularly abundant in the studied algal, bioclastic and sandy material: *Celleporaria palmata*, *Celleporina costazi*, and *Turbicellepora coronopus*. The unidentifiable celleporiform fragments, often relatively numerous, were grouped together in one category.

4.1.3. Vinculariiform

This morphotype has erect rigid colonies with subcylindrical dichotomous branches, cemented by their basis to a solid substrate. This type of colony is abundant in relatively deep waters (40 to 80 m), but may also occupy various shallow-water (<10 m) and sheltered habitats such as cavities within bioherms.

The 30 species belonging to this zoarial type are sometimes very abundant in the material under study (Table 4), above all in the biocalcarenites. These species tend to be dominated by *Idmidronea atlantica* and *Ybselosoecia typica*.

4.1.4. Adeoniform

Forming erect rigid bilaminar colonies, this morphotype is also attached by cementation to a solid substrate. This zoarial form is mostly characteristic of rocky shores, low water energy and relatively slow sedimentation rate. It has an optimum depth of about 40 m to 50 m, but can also live somewhat shallower.

In the Badenian of Hungary, 18 species belong to this colonial morphotype (Table 5), they are particularly numerous in the biocalcarenitic facies. The most abundant are *Metrarabdotos maleckii* and *Smittina cervicornis*.

4.1.5. Reteporiform

This colonial morphotype is characterized by an erect rigid and fenestrate zoarium that generally lives attached by cementation to hard substrates at depths of about 20 to 80 m.

Only three species of this zoarial form occur in the studied material (Table 5). Two of them, *Reteporella beaniana* and *R. cellulosa*, are represented by many fragments in the biocalcarenitic facies.

4.1.6. Cellariiform

This erect flexible morphotype has long segments articulated by chitinous joints. The zoarium itself is attached to loose or solid substrates by its chitinous rootlets. This zoarial form is especially abundant in shallow waters (around 10 m) and, due to its flexibility, is adapted to moderate to high sedimentation rate and energy. It is however also found much deeper.
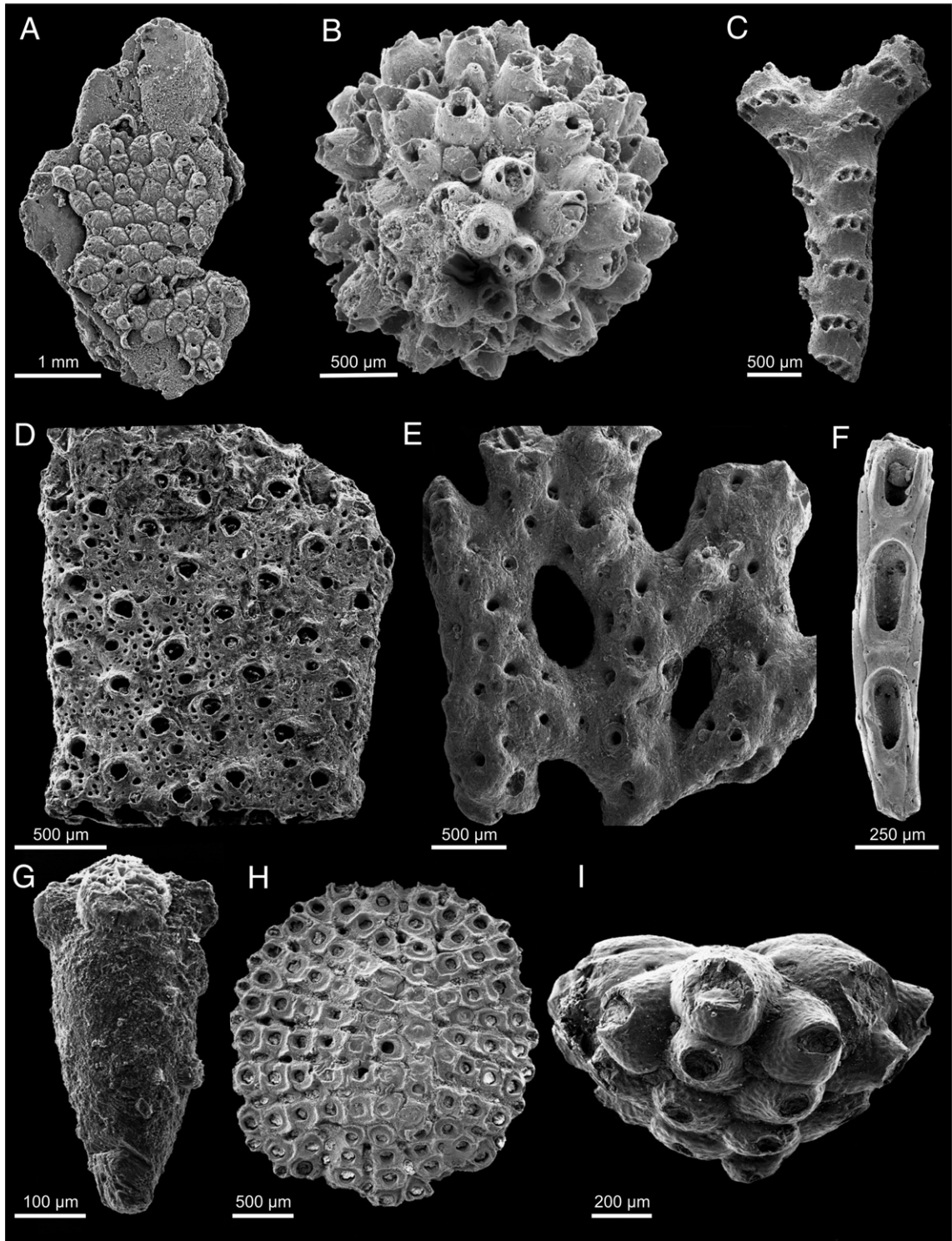
Fig. 3. Scanning electron micrographs of colonial morphotypes encountered in the Badenian of Hungary. A) Membraniporiform (*Puellina kollmanni*); B) Celleporiform (*Celleporina costazi*); C) Vinculariiform (*Pleuronea pertusa*); D) Adeoniform (*Escharina polyomma*); E) Reteporiform (*Reteporella beaniana*); F) Cellariiform (*Nellia oculata*); G) Catenicelliform (*Catenicella elegans*); H) Lunulitiform (*Lunulites androsaces*); I) Conescharelliniform (*Batopora rosula*).

Table 2
List of the membraniporiform bryozoan species represented in the Badenian of Hungary with indication of the facies where they occur

Species	Algae	Corals	Calcarenite	Marls	Sands
Aetea sica * (Couch, 1844)			x		
Alderina nobilis (Reuss, 1848)			x		
Alysidotella sp.					x
Amphiblestrum aff. *trifolium** (Wood, 1844)					x
Annectocyma echinata (Münster in Goldfuss, 1826)	x			x	
Annectocyma major* (Johnston, 1847)	x	x	xx		x
Antropora cf. *granulifera** (Hincks, 1880)					x
Aplousina bobiesi (David and Pouyet, 1974)	x		x		x
Arachnopusia sp.					x
Biflustra savartii* (Audouin, 1826)			x		x
Bobiesipora fasciculata (Reuss, 1848)	x		x		x
Buffonellaria divergens* (Smitt, 1873)	x		xx		
Buffonellodes incisa (Reuss, 1874)	x		x		
Callopora dumerili* (Audouin, 1826)			x		
Callopora fenestrata (Reuss, 1848)	x		x		
Calloporina decorata* (Reuss, 1848)	x	x	x		
Calpensia gracilis (Münster, 1826)			x		
Calpensia nobilis* (Esper, 1796)	x		x	x	x
Cheiloporina campanulata (Cipolla, 1921)	x	x			
Chorizopora brongniarti* (Audouin, 1826)	x		x		
Coleopora insignis (Reuss, 1874)	x				
Conopeum reticulum* (Linnaeus, 1767)					x
Copidozoum tenuirostre* (Hincks, 1880)	x		x		
Cosciniopsis ambita* Hayward, 1974			x		
Crassimarginatella diadema (Reuss, 1848)		x	x		
Crepidacantha odontostoma (Reuss, 1874)	x		x		
Cribella cyclocephala (Reuss, 1874)	x				
Cribellopora latigastra (David, 1949)	x		xx		
Cribrilaria innominata* (Couch, 1844)	x	x	xx		
Cribrilaria rarecostata (Reuss, 1848)			x		
Cribrilina messiniensis Pouyet and Moissette, 1986			x		
Cryptosula pallasiana* (Moll, 1803)			x		
Desmeplagioecia tenuis? (Reuss, 1869)					x
Diplosolen obelium* (Johnston, 1838)	x		x		x
Disporella grignonensis? (Milne Edwards, 1838)					x
Disporella hispida* (Fleming, 1828)	xx		xx		x
Distansescharella seguenzai* Cipolla, 1921			x		
Electra monostachys* (Busk, 1854)	x		x		
Ellisina gautieri* Fernandez Pulp. and Reverter Gil, 1993	x	x			x
Ellisina grandis? Canu and Bassler, 1925					x
Emballotheca longidens (Cipolla, 1921)			x		
Escharella arrecta (Reuss, 1848)			x		
Escharella circumornata (Reuss, 1848)			x		
Escharella peachi* (Johnston, 1847)	x				
Escharella reussiana (Busk, 1859)	x	x	x		
Escharella tenera (Reuss, 1874)			x		
Escharella variolosa* (Johnston, 1838)			x		
Escharina dutertrei* (Audouin, 1826)		x	x		
Escharina vulgaris* (Moll, 1803)	x		x		x
Escharoides coccinea* (Abildgaard, 1806)	x		xx	x	x
Escharoides megalota (Reuss, 1848)	x		x		
Fenestrulina harmelini David and Pouyet, 1972			x		
Figularia haueri (Reuss, 1848)	x				
Figularia manzonii (Reuss, 1874)			x		
Hagiosynodos latus* (Busk, 1856)			x		x
Hemicyclopora collarina Canu and Lecointre, 1925			x		
Herentia hyndmanni* (Johnston, 1847)			x		
Herentia musensis (David and Pouyet, 1976)			x		

Table 2 (*continued*)

Species	Algae	Corals	Calcarenite	Marls	Sands
Heteropora sp.	x		x		
*Hincksina flustroides** (Hincks, 1877)			x		
Hinksina loxopora (Reuss, 1848)			x		
Hincksipora porosa? (Manzoni, 1877)	x				
Hippadenella regularis (Reuss, 1874)	x				
*Hippaliosina depressa** (Busk, 1852)		x	x		x
Hippodiplosia sp.	x				
Hippopleurifera aperta (Reuss, 1874)			x		
Hippopleurifera biauriculata (Reuss, 1848)			xx		
Hippopleurifera binata? (Reuss, 1874)			x		
Hippopleurifera hypsostoma (Reuss, 1874)	x		x		
Hippopleurifera semicristata (Reuss, 1848)	x		x		
Hippopleurifera sp.			x		
Hippoporella bicornis Canu and Lecointre, 1928	x		x		
Hippoporella pauper (Reuss, 1874)	x		x		x
Hippoporina rarepunctata (Reuss, 1848)			x		
Hippoporina sulcifera (Reuss, 1874)	x				
*Hippothoa flagellum** (Manzoni, 1870)			x		
Lacerna fuchsi (Reuss, 1874)			x		
*Lagenipora lepralioides** (Norman, 1868)			xx		
Membraniporella ungeri (Reuss, 1848)			x		
Membraniporidra sp.			x		
Micropora papyracea (Reuss, 1848)	x		x		
Micropora parvicella Canu and Lecointre, 1927			x		
*Microporella ciliata** (Pallas, 1766)	x		x		x
Microporella inamoena (Reuss, 1874)			xx		
*Mollia patellaria** (Moll, 1803)	x		x		
*Monoporella nodulifera** (Hincks, 1881)					x
Oncousoecia biloba (Reuss, 1848)	x		x		x
*Onychocella angulosa** (Reuss, 1848)	x	x	xx		x
Patinella goldfussi (Reuss, 1864)	x		x		x
Patinella mediterranea de Blainville, 1834					x
Patinella prolifera (Reuss, 1848)	x		x		x
*Patinella radiata** (Audouin, 1826)	x		x		x
Patinella stellata (Goldfuss, 1826)			x		
Perigastrella sp.	x				
Phylactella uniserialis (Canu and Bassler, 1925)			x		
*Plagioecia patina** (Lamarck, 1816)	x		x		
*Plagioecia platydiscus** Harmelin, 1976			x		
Plagioecia rotula (Reuss, 1848)	x		x		
*Plagioecia sarniensis** (Norman, 1864)	x		x		
Plagioecia sp.		x			
Porella cheilopora (Reuss, 1848)			x		
Poricella areolata (Reuss, 1874)	x		x		x
Prenantia sp.			x		
Puellina gigantea David, Mongereau and Pouyet, 1972	x		x		
Puellina kollmanni (David and Pouyet, 1974)			x		
Ramphonotus appendiculata (Reuss, 1848)	x		x		
*Reptadeonella violacea** (Johnston, 1847)					x
Rhagasostoma stenostoma (Reuss, 1848)	x		x		
Rosseliana incompta (Reuss, 1874)	x		x		x
Saevitella inermis? Bobies, 1956			x		
*Schedocleidochasma porcellanum** (Busk, 1860)					x
Schismoporella schizogaster (Reuss, 1848)			x		
*Schizobrachiella sanguinea** (Norman, 1868)	x		x		x
*Schizomavella auriculata** (Hassall, 1842)	x		xx		x
Schizomavella aff. *discoidea** (Busk, 1859)			x		
Schizomavella grossipora (Reuss, 1874)		x			

Table 2 (*continued*)

Species	Algae	Corals	Calcarenite	Marls	Sands
Schizomavella tenella (Reuss, 1848)	x		xx		x
Schizoporella dunkeri* (Reuss, 1848)			x		
Schizoporella geminipora (Reuss, 1848)	x		xxx		x
Schizoporella longirostris* Hincks, 1886	x	x	x		
Schizoporella tetragona (Reuss, 1848)			x		xx
Schizoporella unicornis* (Johnston, 1847)	x				x
Schizoporella sp.			x		
Schizotheca fissa* (Busk, 1856)	x		x		
Smittina canavarii (Neviani, 1900)			x		
Smittina sp.			x		
Smittipora platystoma (Reuss, 1848)	x		x		
Smittoidea reticulata* (Mac Gillivray, 1842)			x		
Steginoporella reussi David and Pouyet, 1972	x		x		
Steginoporella tuberculata marg. David and Pouyet, 1979	x		x		x
Steraechmella buski* Lagaaij, 1952			x		
Stomatopora subdivaricata (d'Orbigny, 1852)			x		
Thalamoporella neogenica Buge, 1950	x		x		
Tremopora radicifera* (Hincks, 1881)	x		x		
Trochiliopora beyrichi (Reuss, 1851)			x		x
Trypostega rugulosa (Reuss, 1874)	x		x		
Tubulipora dimidiata (Reuss, 1848)	x		x		x
Tubulipora flabellaris?* (Fabricius, 1780)			x		
Tubulipora foliacea Reuss, 1848			x		
Tubulipora partschi (Reuss, 1848)	x		x		x
Tubulipora pluma (Reuss, 1848)	x		x		x
Tubulipora plumosa?* Harmer, 1898	x		x		
Tubulipora sp. 1	x				
Tubulipora sp. 2	x				
Umbonula austriensis? David and Pouyet, 1974			x		
Umbonula macrocheila (Reuss, 1848)	x	x	x		
Umbonula monoceros (Reuss, 1848)	x		xx		
Vibracella trapezoidea (Reuss, 1848)			x		
Watersipora goniostoma (Reuss, 1848)			x		

Extant species are indicated by an asterisk. The number of crosses is proportional to the approximate abundance of bryozoan fragments.

The cellariiform morphotype is represented in the Badenian of Hungary by many fragments belonging to 14 species and occurring in all facies (Table 6). The most abundant and ubiquitous belong to the genera *Cellaria*, *Crisia*, and *Scrupocellaria*.

4.1.7. Catenicelliform

This other erect articulated morphotype is also attached to hard substrates by chitinous rootlets. However, each very short segment is constituted only of one or two zooids. This zoarial form, adapted to high water energy, is abundant at very shallow depths (0–40 m).

Only two species of this fragile form, both extant, are represented in the studied material by very rare fragments (Table 6).

4.1.8. Lunulitiform

The colonies of this discoidal concavo–convex morphotype live freely on sandy and shelly bottoms. They are especially abundant at depths of about 30 to 60 m.

This zoarial form is represented in the Badenian of Hungary by five species (Table 6). Fragments and even whole colonies of this morphotype are especially abundant in some sandy and argillaceous sandy levels (Dulai, 1995).

4.1.9. Conescharelliform

This small conical type of colony lives attached by chitinous rootlets to muddy bottoms in moderately deep to deep environments (Moissette, 1996).

Only one species (*Batopora rosula*) belonging to this zoarial form is represented here by very rare colonies in some of the marly samples of the Tengelic-2 borehole (Table 6).

4.2. Extant bryozoan species

Many of the species (86 out of 238) identified in this study are extant. Thus, data on the distribution of the bryozoans living in the present-day Atlantic and

Table 3
List of the celleporiform bryozoan species represented in the Badenian of Hungary with indication of the facies where they occur

Species	Algae	Corals	Calcarenite	Marls	Sands
Cellepora globularis Bronn, 1837	x				
Cellepora "*pumicosa*"* (Waters, 1879)			x		
Celleporaria cerioporoides (Canu and Lecointre, 1930)	x		x		x
Celleporaria foraminosa (Reuss, 1848)			x	x	xx
Celleporaria palmata (Michelin, 1847)	x		xxx		x
Celleporina bugei Pouyet, 1973			x		
*Celleporina costazi** (Audouin, 1826)	x	x	xx		x
Celleporina aff. *lucida** (Hincks, 1880)	x				
Celleporina minuscula Pouyet, 1973	x		x		x
Ceriopora tumulifera? (Canu and Lecointre, 1934)			x		
Multigalea (?) sp.			x		
*Omalosecosa ramulosa** (Linnaeus, 1767)			x		x
Reptomulticava parviporosa ? Canu and Lecointre, 1934	x		x		x
Turbicellepora aviculifera (Manzoni, 1877)			x		
*Turbicellepora canaliculata?** (Busk, 1886)	x		x		x
Turbicellepora coarcta (Canu and Lecointre, 1930)			x		
Turbicellepora cf. *compressa** (Busk, 1859)	x		x		
*Turbicellepora coronopus** (Wood, 1844)	x		xxx		x
*Turbicellepora crenulata?** Hayward, 1978					x
Turbicellepora krahuletzi? (Kuhn, 1925)	x				
Turbicellepora sp.					x
Unidentified celleporiforms	xx		xxx		x

Extant species are indicated by an asterisk. The number of crosses is proportional to the approximate abundance of bryozoan fragments.

Mediterranean can be used in palaeoecological and palaeobathymetric reconstructions (Gautier, 1962; Hayward, 1974; Harmelin, 1976; Ryland and Hayward, 1977; Hayward and Ryland, 1979, 1985; Zabala, 1986; Hayward and McKinney, 2002). Many species are practically eurybathic (from 0 down to 100–300 m or even more), but a number of relatively stenobathic species give more precise information, especially when they show an optimum depth range (Fig. 4).

Many extant stenobathic species occurring in the Badenian of Hungary indicate shallow waters (0–30 m). Other species are characteristic of moderately deep environments (30–100 m), whereas a very few are indicative of deeper habitats (100–300 m).

4.3. Statistical analysis

To numerically investigate the inter-assemblage compositional relationships, we selected two distance-based methods for their complementary approaches (e.g., Field et al., 1982): Cluster Analysis and Non-metric Multi-Dimensional Scaling (see Legendre and Legendre, 1998 and references therein concerning these two methods, their relative merits and flaws, and the distinct underlying assumptions about the nature of the similarity structure to be extracted). Indeed, CA basically focuses on the nested compositional relationships between assemblages, whereas NMDS primarily aims at extract-ing intergradational information in a reduced space. Hence, as most biogeographical and ecological patterns actually combine hierarchical and gradational structuring of the taxonomic assemblages, both methods are useful and provide complementary information about the compositional resemblance of the studied assemblages.

4.3.1. Cluster Analysis of the colonial morphotype abundance matrix

We performed a Cluster Analysis of the sampled bryozoan assemblages based on the abundances of the colonial morphotypes (zoarial forms + boring species) described above. Two samples with fewer than 30 fragments (Visegrád3 and Rákos1) were discarded, leading to a data table of 43 samples × 10 colonial morphotypes with the following general characteristics:

– 313,364 colony fragments distributed between 232 (54%) combinations of colonial morphotype assemblages;
– each colonial morphotype is recorded in 1 (coneschar-elliniform, represented in the Tengelic-2 borehole by only 3 colonies) to 43 assemblages (cellariiform, 117,295 fragments corresponding to 37.4% of the complete data set), six of the ten colonial morphotypes occurring with more than 10,000 fragments;
– each assemblage contains 2 to 8 colonial morpho-types, and 32 (Szob3 and Tengelic-2) to 142,315

Table 4
List of the vinculariiform bryozoan species represented in the Badenian of Hungary with indication of the facies where they occur

Species	Algae	Corals	Calcarenite	Marls	Sands
Bobiesipora fasciculata (Reuss, 1848)	x		xx		x
Buskea sp.			x		
Canda rectangulata Udin, 1964	x		xx	x	
Crassimarginatella macrostoma (Reuss, 1848)			x		
Crisidmonea foraminosa (Reuss, 1851)			x		x
Entalophoroecia anomala (Reuss, 1848)	x		xx		
Entalophoroecia clavula (Reuss, 1848)			x		
Entalophoroecia fasciculifera (Canu and Bassler, 1923)	x		x		
*Entalophoroecia gracilis?** Harmelin, 1976	x		x		
Entalophoroecia pulchella (Reuss, 1848)	x		xx		x
*Entalophoroecia robusta?** Harmelin, 1976			x		
Entalophoroecia sp.			x		
*Frondipora verrucosa** (Lamouroux, 1821)	x		x		x
Heteropora sp.	x		x		
*Hornera frondiculata** Lamouroux, 1821	xx		xxx	x	x
*Hornera lichenoides?** (Linnaeus, 1758)			x		
Hornera subannulata Philippi, 1843			xx		
*Idmidronea atlantica** (Forbes in Johnston, 1847)	x		xxxx	x	xx
Idmidronea disticha (Reuss, 1848)			xx		x
*Myriapora truncata** (Pallas, 1766)			x		
*Omalosecosa ramulosa** (Linnaeus, 1767)			x		x
Oncousoecia biloba (Reuss, 1848)	x		x		x
*Palmiskenea skenei** (Ellis and Solander, 1786)			x		
Pleuronea pertusa (Reuss, 1848)	x		xxx	x	x
Polyascosoecia coronopus (Canu and Bassler, 1922)	x		xxx	x	xx
Pseudofrondipora davidi Mongereau, 1970			x		x
Steginoporella cucullata (Reuss, 1848)			xx		
*Tervia irregularis** (Meneghini, 1845)	xx		xx		x
Tetrocycloecia dichotoma (Goldfuss, 1827)			x		xx
Ybselosoecia typica (Manzoni, 1878)	xx		xxxx	x	x

Extant species are indicated by an asterisk. The number of crosses is proportional to the approximate abundance of bryozoan fragments.

(Cserhát8) fragments, corresponding to an exponential distribution of the number of fragments ($R^2 = 0.963$), with median and mean values of 933 and 7,288 fragments, respectively;

– each colonial morphotype-assemblage combination contains 1 to 45,360 fragments representing relative abundances within assemblages ranging from 0.04% to 96.9%, with an exponential distribution of the 194 colonial morphotype-assemblage combinations showing a relative abundance >1% ($R^2 = 0.995$).

First, the relative abundances were transformed using the usual angular transformation $T_{i,k} = \frac{2}{\pi}\sin^{-1}\left(\sqrt{P_{i,k}}\right)$, where $P_{i,k}$ is the proportion, within assemblage i, of colonial morphotype k. For each relative abundance $P_{i,k}$ within a given taxonomical assemblage made of n colony fragments, such transformation (i) makes their mean and variance independent, and (ii) unskews their distribution to a normal variate with expected mean $T_{i,k}$ and associated standard deviation $\sigma_{T_{i,k}} = \sqrt{\frac{2}{\pi}\frac{1}{4n}}$, independent of $T_{i,k}$ (e.g., Sokal and Rohlf, 1995: p. 419–422).

Second, the square-rooted Bray and Curtis' (1957) distance matrix was computed based on the formula:

$$D_{i,j} = \sqrt{\frac{\sum_{k=1}^{k=10} |T_{i,k} - T_{j,k}|}{\sum_{k=1}^{k=10} (T_{i,k} + T_{j,k})}}$$

where $T_{i,k}$ and $T_{j,k}$ are the transformed-proportions, for the colonial morphotype k, of assemblages i and j, respectively. The square root was introduced so that the dissimilarity matrix describes a metrical and Euclidean space, an important prerequisite for Cluster Analysis (Gower and Legendre, 1986; Legendre and Legendre, 1998). Then, the taxonomical similarity structure stored in this distance matrix was extracted and visualized as a phenogram using the Neighbor-Joining algorithm (Saitou and Nei, 1987). NJ is a fast and efficient heuristic algorithm allowing the recovery of the additive tree that minimizes the total sum of (unconstrained) branch

Table 5
List of the adeoniform and reteporiform bryozoan species represented in the Badenian of Hungary with indication of the facies where they occur

Species	Algae	Corals	Calcarenite	Marls	Sands
Adeoniforms					
Adeonella polystomella* (Reuss, 1848)			xx		xx
Buffonellaria divergens* (Smitt, 1873)			x		
Emballotheca longidens (Cipolla, 1921)	x		x		x
Escharina polyomma (Reuss, 1848)			xx		x
Goodonia sp.			x		
Hippopleurifera ampla (Reuss, 1848)			x		
Mesenteripora meandrina (Wood, 1844)			x		
Metrarabdotos maleckii Cheetham, 1968	x		xxx		x
Metroperiella sp.			x		
Pentapora fascialis* (Pallas, 1766)			x		
Porella erecta? David, Mongereau and Pouyet, 1972			x		
Reussia elongata (David, Mongereau and Pouyet, 1972)			x		
Schizostomella grinzingensis David and Pouyet, 1974					x
Smittina cervicornis* (Pallas, 1766)	x		xxxx		x
Smittina cf. *colleti** (Jullien, 1903)			x		
Steginoporella intermedia Buge and David, 1967			x		
Tremopora radicifera* (Hincks, 1881)			x		
Umbonula macrocheila (Reuss, 1848)	x		xx		x
Reteporiforms					
Iodictyum rubeschi (Reuss, 1848)	x		xx		
Reteporella beaniana* (King, 1846)	x		xxx		
Reteporella cellulosa* (Linnaeus, 1767)	x		xxx	x	x

Extant species are indicated by an asterisk. The number of crosses is proportional to the approximate abundance of bryozoan fragments.

lengths (see Felsenstein, 2004). In the case of the present study, such an additive tree reconstruction method is preferable to others, perhaps more usual hierarchical clustering techniques such as Single or Complete Linkage, UPGMA or UPGMC, which assume inter-assemblage compositional transformation rates to be statistically constant through time and space (the "clock hypothesis"), i.e. each leaf (taxonomical assemblage) of the reconstructed tree to be equally distant to the root of the topology (see Lapointe and Legendre, 1992: p. 170–171).

Third, a parametric resampling procedure was applied to the available data in order to estimate the confidence levels associated with each observed cluster of taxonomical assemblages. For each assemblage i and colonial morphotype k, a transformed-proportion pseudo-value $T_{i,k}^*$ was randomly drawn from a Gaussian distribution with mean and standard deviation $T_{i,k}$ and $\sigma_{Ti,k}$, respectively. Then, the resulting pseudo-table of transformed-proportions was analysed in the same way as the observed table (square-rooted Bray–Curtis' distance matrix and Neighbor-Joining clustering). This two-step procedure was reiterated 10,000 times in order to estimate the confidence level associated with each cluster in the observed tree (see Escarguel, 2005 for methodological details). The angular transformation,

Bray–Curtis' distance matrix computation and parametric resampling procedure was achieved using the "ArcSine–Transfo" and "Bray–Curtis" programs of the DISSIM package (Escarguel, 2005); the NJ-tree reconstruction and extraction of the clusters' confidence intervals was carried out using the "Neighbor" and "Consense" programs of the PHYLIP package (Felsenstein, 2005).

4.3.2. Non-metric multidimensional scaling of the species occurrence matrix

We applied a NMDS to the 45 assemblages × 238 specific taxa (+1 for unidentified celleporiforms) incidence (presence/absence) table corresponding to the full, taxonomically standardised information available. The general characteristics of this data set are as follows:

– 1,464 recorded occurrences, representing 13.6% of all possible taxon-assemblage couples;
– each taxon recorded in 1 (68 species) to 34 (*Crisia denticulata*) assemblages, corresponding to an exponential distribution of the number of occurrences ($R^2 = 0.967$), with median and mean values of 3 and 6.12 assemblages, respectively;
– each assemblage containing 4 (Rákos1 and Szob 1) to 105 (Cserhát8) taxa, corresponding to an exponential

Table 6
List of the cellariiform, catenicelliform, lunulitiform, and conescharelliniform bryozoan species represented in the Badenian of Hungary with indication of the facies where they occur

Species	Algae	Corals	Calcarenite	Marls	Sands
Cellariiforms					
Cellaria fistulosa (Linnaeus, 1758)			xxxx	x	xxx
Cellaria salicornioides Lamouroux, 1816	xxx		xxxxx	x	xx
Crisia denticulata (Lamarck, 1816)	xxx	x	xxxxxx	x	xx
Crisia eburnea (Linnaeus, 1758)	xxx	x	xxxxx	x	xx
Crisia elongata Milne Edwards, 1838		x			
Crisia haueri (Reuss, 1848)	x		xxx	x	x
Crisia hoernesi Reuss, 1848	x		xxxx	x	x
Crisia lecointrei Bobies, 1958			x		
Gemellipora eburnea Smitt, 1873				x	
Margaretta cereoides (Ellis and Solander, 1786)	x		xx		x
Nellia oculata Busk, 1852	x				xx
Scrupocellaria bertholleti? (Audouin, 1826)			xx		
Scrupocellaria elliptica (Reuss, 1848)	xx		xxx		x
Scrupocellaria sp.			x		
Catenicelliforms					
Catenicella elegans Busk, 1852	x		x		x
Savignyella lafonti (Audouin, 1826)			x		
Lunulitiforms					
Cupuladria vindobonensis Bałuk and Radwanski, 1984				xx	x
Cupuladria sp.					x
Lunulites androsaces Michelotti, 1838				x	x
Reussirella haidingeri (Reuss, 1848)			x	xx	xx
Stenosipora simplex (Koschinsky, 1885)			x		
Conescharelliniforms					
Batopora rosula (Reuss, 1848)				x	

Extant species are indicated by an asterisk. The number of crosses is proportional to the approximate abundance of bryozoan fragments.

distribution of the taxonomic richness ($R^2 = 0.987$), with median and mean values of 24 and 32.5 taxa, respectively.

We computed the dissimilarity matrix associated with this incidence table by using the non-metric coefficient of Watson et al. (1966; noted D_{13} by Legendre and Legendre, 1998: p. 286):

$$D_{i,j} = \frac{E_i + E_j}{N_i + N_j} = 1 - \frac{2 \times C_{i,j}}{N_i + N_j},$$

where E_i and E_j are the number of taxa observed only in assemblages i and j, respectively, N_i and N_j are the total number of taxa in assemblages i and j, respectively, and $C_{i,j}$ is the number of taxa shared by assemblages i and j. This semi-metric coefficient is the 1-complement of the Dice (or Sørensen) coefficient of similarity; it corresponds, for binary data, to the Bray–Curtis coefficient. We prefer this semi-metric coefficient to other metric and perhaps more classical ones (e.g., the Simpson and Jaccard coefficients) for the double weight given to shared presences, and thus relative under-weighting of absence as an indication of faunal differences. As already emphasised by Legendre and Legendre (1998: p. 256), such relative over-weighting of double presences is an appealing property due to the always ambiguous meaning of absence, which does not necessarily reflect "real" differences between the compared taxonomic assemblages.

The ordination of the objects (taxonomical assemblages) in two dimensions was achieved using the algorithm implemented in PAST, v. 1.54 (Hammer et al., 2001), by selecting the Bray–Curtis index. The analysis was performed 5×10 times in order to enhance the probability that the algorithm actually converged towards the "best" solution (i.e., the ordination with lowest associated stress-value).

5. Facies analysis

On the basis of the observed sedimentological and palaeontological features five facies have been differentiated
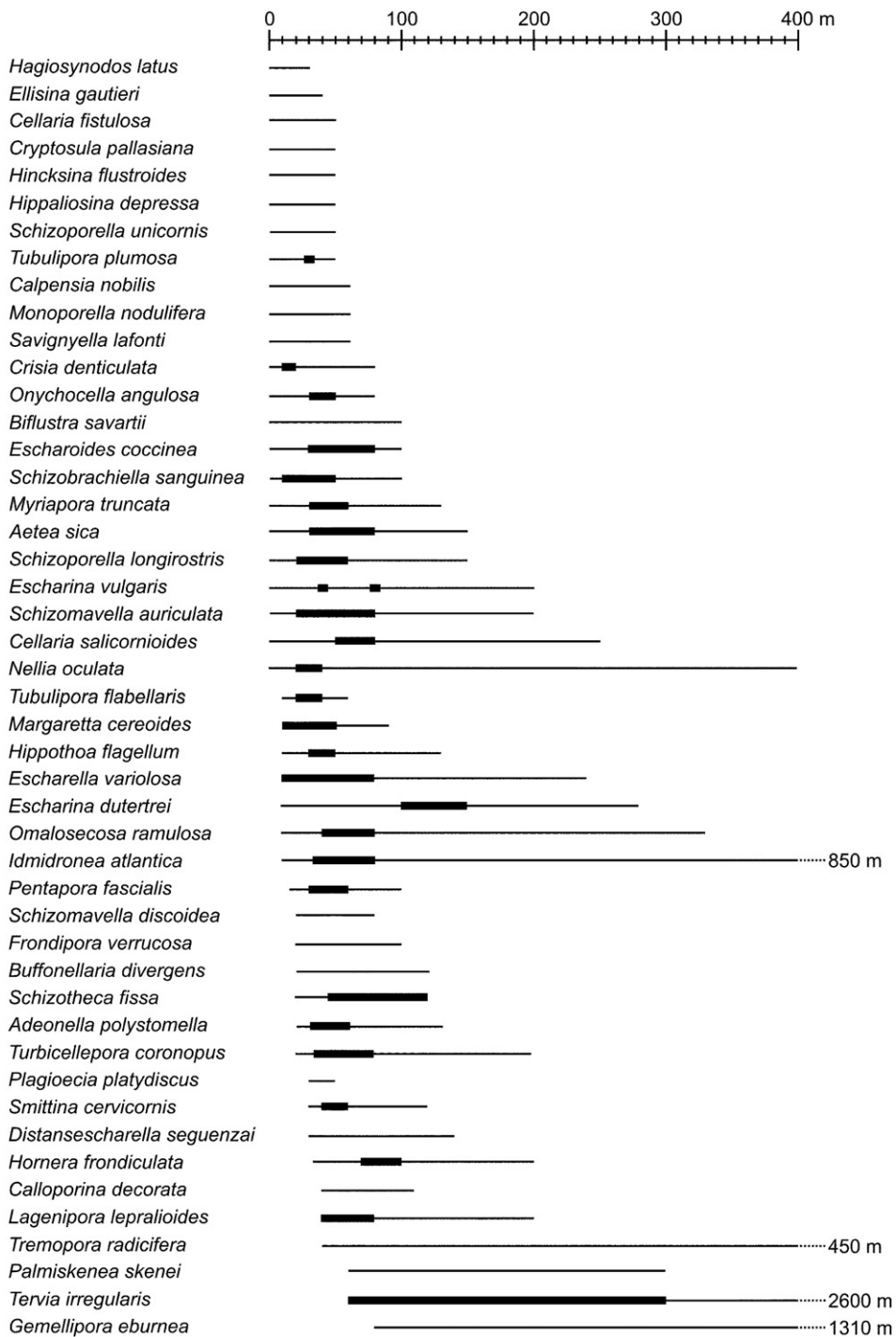
Fig. 4. Present-day known depth ranges and bathymetric optima (indicated by thick lines) of some extant stenobathic bryozoan species found in the Badenian deposits of Hungary.

(see Tables 2–6 and the text accompanying the description of the zoarial forms for the distribution of each bryozoan species into these facies). A gradient

from almost pure limestone to marl is in fact observed, with ubiquitous red algal remains, excepted in the Tengelic marls.

5.1. Coral buildups

Small coral patch reefs and/or biostromes were relatively common throughout the Central Paratethys during the Badenian (Rögl and Steininger, 1983; Pisera, 1996; Randazzo et al., 1999; Riegl and Piller, 2000; Saint Martin et al., 2000; Górka, 2002). The hermatypic scleractinians involved belong to a limited number of species and genera (mostly *Porites* and *Tarbellastraea*). Coralline algae and microbial crusts also play an important role in the construction of the reef framework (Saint Martin et al., 2000; Górka, 2002; Radwanski et al., 2006). Bryozoans are neither abundant, nor diverse (18 species) in the sampled coral facies. Most are encrusting (Table 2) and only some of them can be considered as accessory framework builders. A lesser number of erect articulated species (*Crisia* spp.) also occur in the associated sediment, together with very rare adeoniform colonies (*Smittina cervicornis*) and small celleporids (*Celleporina costazi*).

The coral patch reefs we studied in Hungary (Fig. 2) are situated in and around Budapest: Diósd, Visegrád (coral facies), and Rákos. Only three samples were collected from this facies.

5.2. Coralline algal limestones

Shallow-water Cenozoic to Recent marine deposits often contain abundant encrusting, branching, nodular and geniculate red algae (e.g., Bosence, 1983a; Braga and Aguirre, 2001; Halfar and Mutti, 2005). This is also the case in the Badenian of Hungary where bryozoans occurring together with numerous calcareous algae are much more abundant and diverse (115 species) than in the coral facies. Here as well the most abundant colonial morphotype is the membraniporiform (Table 2), but a relatively rich assemblage of celleporiform and erect colonies (Tables 3–6) always accompanies it.

Although associated with most other facies in the studied outcrops, coralline algae predominate at some localities (Fig. 2) where they form relatively well-defined structures or accumulations of rhodoliths: Mecsek, Rákos, Törökmező, Visegrád (red algal facies), Zebegény. A total of 12 samples were collected from this facies.

5.3. Biocalcarenites

This facies is characterized by the abundance of more or less fragmented calcareous skeletal remains, mostly coralline algae, molluscs, bryozoans, and to a lesser extent echinoderms. In this facies, bryozoans are both very abundant (in volume and number of colonies and fragments) and diverse (200 species, up to 105 species in one of the samples). Almost all colony types are represented with the most characteristic and frequent species belonging to the celleporiform, reteporiform, vinculariiform, and adeoniform morphotypes (Tables 2–6).

Numerous samples (15) correspond to this facies. They were taken from 8 different localities: Diósd, Fertőrákos, Kemence, Mátraszőlős, Mátraverebély, Őrs vezér tere (upper part, sample 5), Sámsonháza, and Visegrád (Fig. 2).

5.4. Sands and sandstones

More or less indurated quartzose sands contain skeletal remains belonging mostly to molluscs and bryozoans. The granulometry varies from fine-grained and argillaceous (Szob) to coarse-grained (Várpalota) and even gravely (Borsodbóta). In this facies, bryozoans are not very abundant and their diversity is also relatively moderate (91 species). However, with the exception of the conescharelliniform, all zoarial types occur in this facies (Tables 2–6). The assemblage is dominated by the lunulitiforms and to a lesser extent by the cellariiforms.

The sandy, more or less argillaceous, material we studied in the Badenian of Hungary was sampled from four sections: Borsodbóta, Őrs vezér tere (lower part, samples 1–4), Szob, and Várpalota (Fig. 2). Ten samples were collected from this facies.

5.5. Marls

In this study the marly facies is limited to the boreholes drilled near the villages of Tengelic and Szokolya (Fig. 2). At Tengelic, the argillaceous material is characterized by the abundance of benthic and planktonic foraminifer shells (Báldi, 1997; Báldi et al., 2002; Báldi, 2006). Nevertheless, with only 22 species, bryozoans are neither abundant, nor diverse, in this facies. The assemblage of zoarial types (Tables 2–6) is principally characterized by the co-occurrence of lunulitiforms and vinculariiforms (Szokolya) or vinculariiforms and conescharelliniforms (Tengelic). The adeoniforms and the celleporiforms are noticeably absent, the membraniporiforms and reteporiforms extremely scarce, and the cellariiforms relatively rare.

The deep-water *Batopora rosula* (conescharelliniform: Moissette, 1996) and *Gemellipora eburnea* (cellariiform) are probably the most characteristic species of this facies in the Tengelic-2 borehole material. However, with abundant lunulitiforms in a more sandy material, the bryozoans from the Szokolya borehole

indicate shallower depositional environments. A total of 28 samples were collected from this facies, but each of them contains only a very small number of bryozoan colonial fragments (Tables 2–6).

6. Results of the palaeontological and statistical analyses

Combining the different analytical methods presented above allows us to identify several groups of localities based on their bryozoan contents and sedimentological features.

6.1. Cluster analysis

The tree resulting from the Cluster Analysis is given in Fig. 5. Labels indicating the interpreted environment for each of the clusters are added to the output graph. The Bray–Curtis' distance matrix computed from the observed data table and corresponding to this consensus topology is independent of the matrix of standardised differences in taxonomic richness (BC = $0.015 \times \delta_{TR}$ +

0.65, $R^2 = 6 \times 10^{-4}$) and number of fragments (BC = $0.076 \times \delta_{NF} + 0.60$, $R^2 = 0.015$) (see Maridet et al., in press for a definition and methodological considerations about δ). Such independence clearly indicates that the identified clusters of assemblages are not a direct consequence of inter-assemblage differences in taxonomic richness or sampling intensity.

Table 7 gives the mean relative abundances of each colonial morphotype in the seven identified main clusters. For each colonial morphotype, atypically high or low proportions characterize each cluster.

6.1.1. Cluster A
This shows high proportions of celleporiforms, vinculariiforms, and cellariiforms. Membraniporiforms are very rare. This cluster appears to be related to the sandy, relatively coarse-grained facies. It corresponds to shallow-water environments on a terrigenous platform.

6.1.2. Cluster B
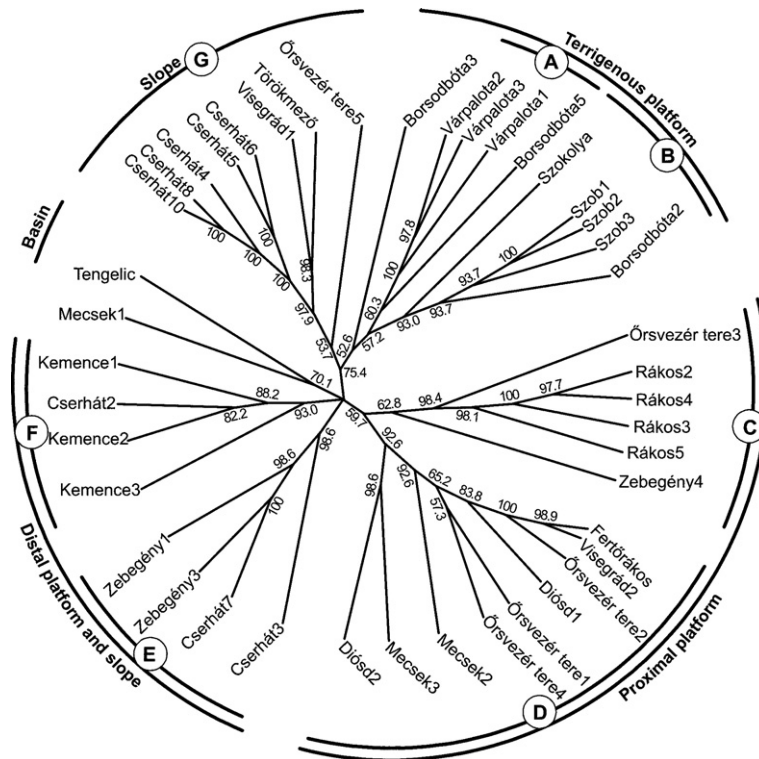This is characterized by very high proportions of lunulitiforms, together with exceptionally low amounts of

Fig. 5. Consensus NJ-tree corresponding to the square-rooted Bray–Curtis' distance matrix computed from the 43 assemblages × 10 colonial morphotype abundance table; percentages at nodes are bootstrap confidence intervals estimated using a parametric random resampling procedure with 10,000 iterations (see text for details). Branch lengths are for graphic convenience only. Circled letters A–G refer to the main clusters of assemblages described and discussed in the text.

Table 7
Mean relative abundances (in %) of each colonial morphotype in the seven main clusters identified in Fig. 5

	A	B	C	D	E	F	G
Membraniporiform	0.57	1.18	9.84	54.88	1.16	1.91	6.51
Celleporiform	14.78	4.21	0.29	5.60	1.01	1.98	7.74
Vinculariiform	42.04	2.23	1.29	3.16	10.53	27.62	18.94
Adeoniform	4.72	4.37	0.07	0.72	2.46	2.17	6.90
Reteporiform	<0.01	0.06	0.10	0.17	5.67	7.79	26.91
Cellariiform	31.66	7.79	85.84	26.29	78.29	57.33	27.24
Catencelliform	<0.01	<0.01	<0.01	0.06	<0.01	<0.01	<0.01
Lunulitiform	0.95	67.29	<0.01	<0.01	<0.01	<0.01	<0.01
Conescharelliniform	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Boring	0.96	0.20	<0.01	<0.01	<0.01	<0.01	<0.01

For each cluster, characteristically elevated percentages have been highlighted.

cellariiforms. This cluster includes samples collected from the sandy argillaceous facies. It indicates moderate depths of about 30 to 60 m and silty to sandy muddy bottoms where free-living lunulitiform colonies generally thrive.

6.1.3. Cluster C

The proportions of cellariiforms are particularly high in this cluster, which is also characterized by moderate amounts of membraniporiforms. Sites from the coralline algal limestones are grouped together in this cluster interpreted as corresponding to shallow-water carbonate platforms.

6.1.4. Cluster D

This is composed of numerous membraniporiforms, moderately abundant cellariiforms, and extremely low proportions of adeoniforms. This cluster brings together biocalcarenite, algal and coral buildup samples from shallow carbonate platforms.

6.1.5. Cluster E

High proportions of cellariiforms and moderate amounts of vinculariiforms characterize this cluster that includes samples from the biocalcarenite and coralline algal facies. They correspond to moderately deep distal carbonate platform environments.

6.1.6. Cluster F

This consists of abundant vinculariiforms and cellariiforms, although reteporiforms are also relatively numerous. This cluster groups together samples collected from the biocalcarenite facies and represents relatively deep environmental conditions of the slope. This interpretation is further corroborated by the abundance of species such as *Idmidronea atlantica* or *Tervia irregularis*, based on the known depth ranges of these species at the present-day.

6.1.7. Cluster G

This is characterized by the highest percentage of reteporiforms, but cellariiform and vinculariiform fragments are also fairly numerous. Most samples are from the biocalcarenite facies, although one sample from the algal facies also occurs. This cluster is interpreted as deposited on the slope, even if samples from shallower, but rather distal environments (Törökmező and Visegrád1) are also included, as suggested by the relatively higher abundance of membraniporiforms and lower abundance of adeoniforms in these two samples.

Thus, based on the environmental characteristics associated with each colonial morphotype (see above), these seven, significantly supported clusters of assemblages can be related to four types of palaeoenvironments: terrigenous platform (clusters A–B), proximal platform (clusters C–D), distal platform to slope (clusters E–F) and slope (cluster G). The terrigenous platform cluster divides itself into two groups possibly corresponding to more sandy (cluster A) and more argillaceous (cluster B) palaeoenvironments. Clusters C and D mainly differ in their proportions of membraniporiforms and cellariiforms, indicating that they correspond to shallow environments with high (C) and low (D) sedimentation rates, respectively. The Tengelic assemblage clusters with the Mecsek1 one and joins the tree through an unresolved basal polytomy with 8 other assemblages (clusters E and F) corresponding to deeper platform (cluster E), slope (cluster F+Mecsek1) and basin (Tengelic) sedimentary conditions. Concerning clusters E, F and G, the mean relative abundance differences in membraniporiforms (E≈F<G), celleporiforms (E≈F<G), vinculariiforms (E<G<F), reteporiforms (E≈F<G), and cellariiforms (E>F>G) suggest that these three groups characterize relatively high (E), intermediate (F) and relatively low (G) sedimentation rates.

6.2. Non-metric multidimensional scaling analysis

The results of the NMDS are given in Fig. 6. The two ordination axes (OA_1 and OA_2) show weak to moderate logarithmic relationships with taxonomic richness ($OA_1 = -0.091 \times \ln(TR) + 0.286$, $R^2 = 0.52$; $OA_2 = 0.049 \times \ln(TR) - 0.155$, $R^2 = 0.21$) and number of fragments ($OA_1 = -0.021 \times \ln(NF) + 0.139$, $R^2 = 0.16$; $OA_2 = 0.021 \times \ln(NF) - 0.135$, $R^2 = 0.22$). This strongly suggests that the NMDS-first plane is not a direct by-product of the inter-assemblage variation in sampling intensity. Furthermore, it indicates that differences in taxonomic richness (either real or artefactual) are not the only drivers of the relative location of each assemblage on this first plane, and most particularly on the second ordination axis. It is worth noting that this lack of strong dependence is indirectly confirmed by the excellent overall congruence between NMDS and CA results (see below), the observed NJ-tree being shown to be statistically independent of inter-assemblage variations in taxonomic richness or sampling intensity.

Indeed, the major groupings evidenced by CA on the basis of colonial morphotype abundances also appear on the NMDS-first plane generated from the taxonomic occurrence record. A clear palaeoenvironmental struc-

turing of this plane emerges, with groups of taxonomical assemblages characteristic of platform, slope or basin conditions. Concerning the platform assemblages, three sub-groups can even be identified on the basis of their second OA coordinate: proximal platform (low OA_2-value), distal platform (intermediate OA_2-value), and platform with more terrigenous (sandy or argillaceous) sedimentary conditions (high OA_2-value), consistent with OA_2-values obtained for assemblages of the slope. Interestingly, the weakly supported CA-locations of Borsodbóta3 within the terrigenous platform cluster and of Őrsvezér tere5 within the slope cluster G, agree well with the NMDS results.

6.3. Comparison between CA and NMDS results

Both cluster analysis of the colonial morphotype abundances and non-metric multidimensional scaling of the taxonomic incidences produce comparable groupings. A close comparison between CA and NMDS results indicates that only 4/43 of the assemblages are classified differently by these two methods:

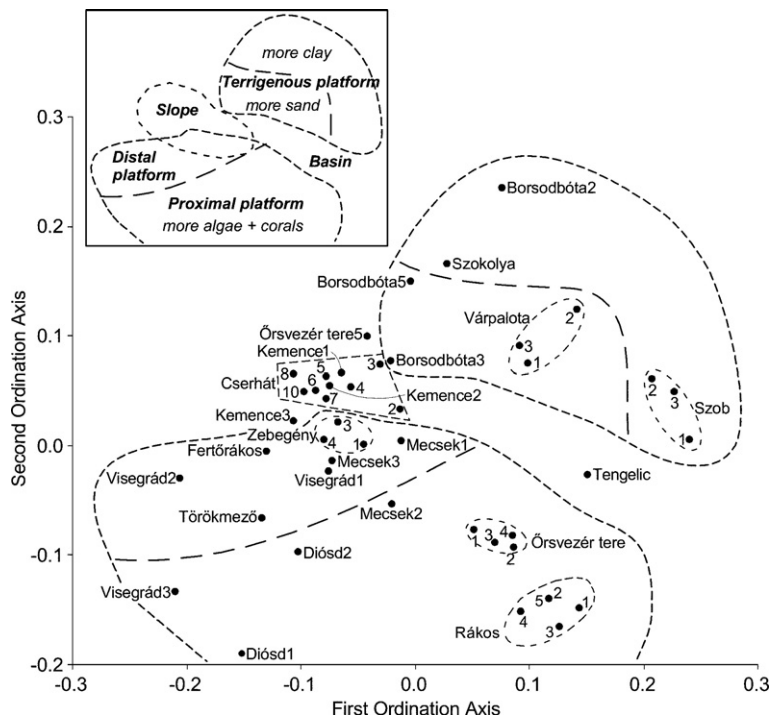– Zebegény4 (941 fragments, 44 taxa), interpreted as a proximal platform assemblage with high sedimentation

Fig. 6. NMDS-first plane corresponding to the non-metric coefficient dissimilarity matrix computed from the 45 assemblages × 238 specific taxa (+1 for unidentified celleporiforms) incidence (presence/absence) table (associated stress-value: 0.165). Inset shows the palaeoenvironmental interpretation of the NMDS-first plane structuring.

rates by CA, and as a distal platform to slope assemblage by NMDS;

– Fertőrákos (933, 76), Visegrád2 (115, 30) and Mecsek3 (1053, 43), interpreted as proximal platform assemblages with low sedimentation rates by CA, and as distal platform to slope assemblages by NMDS.

Hence, these four assemblages have a colonial morphotype signature suggesting shallower environments than their associated taxonomical signature. On the one hand, biological and/or environmental reasons for such discrepancy are not obvious. On the other hand, a quality analysis (Guénoche and Garreta, 2001) of the CA-results strongly suggests that these four localities could actually be misplaced in the consensus NJ-tree. Indeed, while the whole consensus tree appears in good topological agreement with the observed Bray–Curtis' distance matrix (rate of well-designed quadruples: $Rq = 0.71$, compatible with the mean simulated Rq-values for an Euclidean distance given by Guénoche and Garreta's (2001) Table 2), these four assemblages are characterized by atypically high rates of ill-designed quadruples (Zebegény4: 0.323; Fertőrákos: 0.301; Visegrád2: 0.309; Mecsek3: 0.290; mean observed I-DQ: $0.247 \pm 6.8 \times 10^{-3}$). Such values indicate that the location of these assemblages in the consensus NJ-tree is based on contradictory inter-assemblage similarity evidences, generating unusually high numbers of topological inconsistencies. Consequently, following the NMDS-result, we will consider that these four assemblages are best viewed as distal platform to slope rather than proximal platform assemblages.

7. Discussion

7.1. Palaeoenvironmental reconstruction

Based on the palaeoecological (zoarial form and extant species), facies and statistical analyses, four main types of environments have been identified within a mixed carbonate–siliciclastic depositional system.

The palaeoenvironmental reconstruction (Fig. 7) appears quite robust to taphonomical problems classically associated with the constitution of fossil bryozoan assemblages (Lagaaij and Gautier, 1965; Hageman et al., 1997; Moissette, 2000; Amini et al., 2004; Taylor et al., 2004). Indeed, the skeletal material for the present study is mainly or entirely fragmented, whole colonies being unusual. However, some of the colony types (erect, especially flexible) may break down into numerous pieces, whereas others (encrusting and nodular) are pre-

served almost intact. This means that some zoarial forms may easily disintegrate after the death of the colony and become fragmented. Their proportions in a given fossil assemblage may consequently be under or over represented. Nevertheless, the palaeoenvironmental signal captured by the presence/absence data set – which is obviously robust to this fragmentation problem – is almost identical to the signal captured by the zoarial form abundance data set. This indicates that colonial morphotype under- or over-representation actually does not strongly alter the inter-assemblage compositional similarity structure, an important result in terms of palaeoenvironmental reconstruction.

Furthermore, transport across the seafloor by tidal and wave action from shelf environments into deeper or conversely shallower settings cannot be excluded. Nevertheless, the high palaeoenvironmental internal consistency of the analysed data set – leading to high clusters' support values on the consensus tree (Fig. 5) – suggests that such transport, generating local mixtures of faunas with contrasting palaeoenvironmental signatures, is not likely to have played a significant role in the make up of the studied fossil assemblages.

7.1.1. Carbonate platform

As indicated by the great number of membraniporiform colonies and species (about 63% of the total fauna), most of the studied material was deposited in shallow to very shallow waters. This is confirmed by the presence of some catenicelliform species and especially by the known bathymetric distribution of various extant bryozoans (Fig. 4). The shallowest environments are those of the coral reefs (0–20 m), followed, somewhat deeper, by some of the biocalcarenite deposits (Fertőrákos, Visegrád, around 30 m) and by the coralline algal facies (10–60 m).

7.1.2. Slope

The biocalcarenite facies yielded the richest bryozoan faunas: with the exception of conescharelliniforms (occurring only in the marly facies), all colonial morphotypes are represented by numerous colonies and species. Corresponding to mostly quiet environments, the depth of deposition of the deepest biocalcarenite samples, where erect morphotypes predominate, is estimated at about 80 m (Kemence, Cserhát).

7.1.3. Terrigenous platform

The sands and sandstones correspond either to beach environments where skeletal remains from various depth intervals accumulated (Várpalota), or to depressions receiving material from the upper shelf (Borsodbóta), or
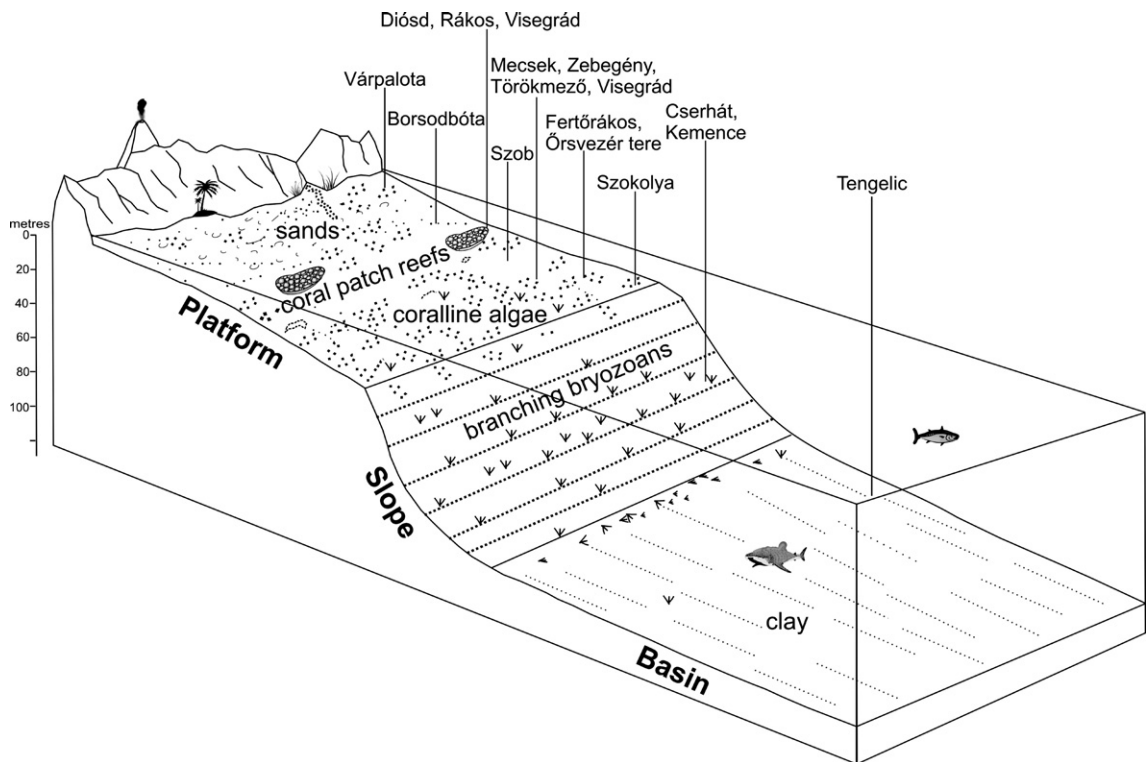
Fig. 7. Idealized palaeoenvironmental reconstruction of the Badenian of Hungary (not to scale and geographic location of sites arbitrary).

to quieter environments where in situ faunas lived (Szob, Szokolya). The last two types of sandy deposits are characterized by the occurrence of numerous lunulitiform colonies whose larvae attach themselves to sand grains or small shell fragments. On the basis of the known bathymetric requirements of the zoarial forms and extant species occurring in this facies, it can be estimated that deposition took place at depths between a few metres to about 30–60 m.

7.1.4. Basin

In contrast, the marly facies is characterized by its very low biodiversity and the small number of bryozoan fragments. Nodular and bilaminar colonies are absent and the encrusting and fenestrate colonial morphotypes very scarce. They are replaced in the Tengelic-2 borehole by a small number of vinculariiform and cellariiform fragments and very few conescharelliniform colonies (*Batopora rosula*). These features indicate quiet and relatively deep depositional environments of about 100 to possibly 300 m (Moissette and Spjeldnaes, 1995; Moissette, 1996, 2000). This is supported by an analysis of the foraminifers indicating water depths of around 200 m and even 600 m (Báldi, 1997; Báldi et al., 2002).

7.2. Palaeoclimate

Alongside numerous warm-temperate to temperate species, mostly those belonging to the Atlantic/Mediterranean biogeographic group, a number of warm-water bryozoan taxa have also been found in the Badenian of Hungary (Moissette et al., 2006). These genera or species only occur in the tropical regions of present-day oceans, but most of them were present in the Mediterranean/Paratethys realm during the Miocene, the Pliocene, and even for some of them during the Pleistocene (Poluzzi, 1975; Barrier et al., 1986; Pouyet and Moissette, 1992; Moissette, 1993; Moissette et al., 1993; Moissette and Saint Martin, 1995; Haddadi-Hamdane, 1996; Moissette, 2000; Pouyet, 2000; Moissette et al., 2002). The following 19 tropical species are represented in the Badenian of Hungary: *Antropora* cf. *granulifera*, *Arachnopusia* sp., *Biflustra savartii*, *Canda rectangulata*, *Catenicella elegans*, *Crepidacantha odontostoma*, *Emballotheca longidens*, *Metrarabdotos maleckii*, *Nellia oculata*, *Polyascosoecia coronopus*, *Schedocleidochasma porcellanum*, *Scrupocellaria bertholleti*, *Steginoporella cucullata*, *S. intermedia*, *S. reussi*, *S. tuberculata margarittae*, *Thalamoporella*

neogenica, *Poricella areolata*, and *Tremopora radici-fera*. Most of these species have been also reported from other Badenian basins of the Central Paratethys (Vávra, 1980; Schmid, 1991; Zágoršek and Holcová, 2005).

Other marine warm-water organisms were recorded from the Badenian of Hungary and more generally of the Central Paratethys: larger benthic foraminifers (*Amphistegina*, *Borelis*, *Heterostegina*: Rögl and Brandstätter, 1993; Rögl, 1998; Bicchi et al., 2003), molluscs (*Isognomon*, *Conus*, *Macrochlamis*, *Megacardita*, *Strombus*: Saint Martin et al., 2000; Harzhauser et al., 2003), hermatypic corals (Hegedűs, 1970; Scholz, 1970; Bałuk and Radwanski, 1977; Oosterbaan, 1990; Pisera, 1996; Riegl and Piller, 2000; Saint Martin et al., 2000; Górka, 2002), decapod crustaceans (Müller, 1984; Górka, 2002; Radwanski et al., 2006), irregular echinoids (*Clypeaster*, *Eucidaris*: Schmid et al., 2001; Kroh, 2003), and fishes (Bellwood and Schultz, 1991; Schmid et al., 2001).

Continental vegetation and terrestrial vertebrates of Central Europe also indicate a warming trend culminating in the Mid-Miocene Climatic Optimum (Nagy, 1992; Ivanov et al., 2002; Böhme, 2003; Jimenez-Moreno et al., 2005; Mosbrugger et al., 2005; Uhl et al., 2006).

However, and as previously reported by Moissette et al. (2006), 110 bryozoan species occur only in Early Badenian deposits, 105 species are found in both Early and Late Badenian, whereas 23 are limited to the Late Badenian (even though the number of Late Badenian localities is relatively small). This general diversity decrease is accompanied by the almost total absence of tropical taxa from Late Badenian sediments where only three such species occur. A similar impoverishment in hermatypic corals is observed (Müller, 1984; Oosterbaan, 1990; Pisera, 1996; Saint Martin et al., 2000). This may indicate a less than optimal climate or a more pronounced isolation of the Badenian sea from the oceanic waters leading to changes in the palaeoceanography of the Paratethys (Müller, 1984; Kókay, 1985; Pisera, 1996; Báldi, 1997, 2006; Moissette et al., 2006).

7.3. The skeletal assemblage concept

Various skeletal assemblage classifications have been devised to characterize carbonate deposits. The resulting assemblages are given contracted names (Hayton et al., 1995). The following assemblages are represented in the Badenian of Hungary: bryomol (bryozoans and molluscs: Nelson et al., 1988b), rhodalgal (rhodophyta = red algae: Carannante et al., 1988), and chlorozoan (chlorophyta = green algae and zoantharia = corals: Lees and

Buller, 1972). James (1997), in an attempt to focus on light dependency and nutrient requirements of the major biotic constituents, also proposed two new terms for these carbonate assemblages: heterozoan (red algae, benthic foraminifers, echinoids, bivalves, and bryozoans) and photozoan (calcareous green algae, benthic foraminifers, zooxanthellate corals, and minor amounts of coralline red algae). The name coralgal (zooxanthellate corals and calcareous algae) is also commonly used as an equivalent of chlorozoan and photozoan. These skeletal carbonate assemblages have often been used as a proxy for palaeotemperature and palaeolatitude. This oversimplification clearly neglects the numerous other factors controlling the distribution of carbonate-producing biota: water depth, substrate, competition, salinity, nutrient levels, etc. (Lees and Buller, 1972; Carannante et al., 1988; Pomar et al., 2004).

During the Early Badenian, localities such as Kemence, Mátraszőlős, Mátraverebély, and Sámsonháza abound in bryozoans, whereas their temporal counterpart, Visegrád, displays reefs with a diverse hermatypic coral fauna. The same is true for the Late Badenian, when deposits rich in bryozoans, molluscs and red algae (Fertőrákos, Őrsvezér tere) are coeval with coral reefs (Diósd, Rákos). How could the two facies types, bryomol and chlorozoan/coralgal, coexist within such a short distance in the Badenian of Hungary? Or, otherwise stated, how can we distinguish between the effects of depth, temperature, and nutrients?

7.3.1. Water depth

Bathymetric variations are a common cause referred to when discussing changes from photosynthetic to heterotrophic communities. Depending notably on light availability, corallinacean algae are able to form rhodoliths at a wide variety of depths, down to more than 150 m (Bosence, 1983b; Iryu et al., 1995; Basso, 1998; Foster, 2001). Carbonate platforms can cope even with the most rapid (e.g. post-glacial) eustatic sea-level rise. The drowning of shallow-marine carbonate-producing areas must therefore be connected either to very rapid tectonic subsidence or to nutrient excess (Hallock and Schlager, 1986).

The bryozoan community of the richest Hungarian locality, Mátraverebély, lived at depths of about 80 m, conspicuously overlapping the depth interval of rhodoliths. Therefore, bathymetric change between successive coralgal and bryomol facies can be excluded.

7.3.2. Temperature

Bryozoan-rich sediments are generally considered to be indicators of non-tropical deposition at the present-

day (Taylor and Allison, 1998). Exceptions to this rule are known (e.g., Pomar et al., 2004; John and Mutti, 2005; Halfar et al., 2006) where bryozoan-dominated sand is formed under (sub)tropical conditions. Nevertheless, it is sometimes difficult to distinguish in these studies between deposition in the geographically-defined tropics (i.e. formed at latitudes between 23.5° N and 23.5° S) and regions outside the true tropics in which tropical-type facies may exist.

Indirect temperature estimates by plant macrofossils (Uhl et al., 2006; Erdei et al., in press), pollens (Nagy and Kókay, 1991; Nagy, 1992; Jimenez-Moreno et al., 2005), and vertebrates (Böhme, 2003) suggest a subtropical to warm-temperate climate for the Central Paratethys during the Badenian. Flourishing contemporaneous coral reefs and warm-water marine invertebrates hint at subtropical temperatures of the sea, certainly above the 18 degrees winter minimum threshold. Seemingly cool-water carbonates identified by Randazzo et al. (1999) result from a mechanical assignment of algal-dominated carbonates and rarity of hermatypic corals to the cool temperate climate zone. An extensive documentation of the cool-temperate carbonate depositional zone by Henrich et al. (1995) emphasizes the lack of hermatypic corals and dasycladacean algae: only the latter is true for the Central Paratethys.

7.3.3. Nutrients

High organic productivity in surface waters is known to reduce phototrophic carbonate production of calcareous algae and zooxanthellate corals (Hallock and Schlager, 1986). Inhibition is caused by light-scattering effects of phytoplankton blooms, significantly reducing water transparency and thus the depth of the euphotic zone. Bryozoans can thrive mostly when their competitors in carbonate production (zooxanthellate corals and algae) are excluded. A reduced euphotic zone might bring about this effect (Lukasik et al., 2000; Pomar, 2001; Mutti and Hallock, 2003; Halfar et al., 2006). Photosynthetizer-dominated communities are common in oligotrophic and lower mesotrophic environments: coral reefs are examples of the first and algal meadows are typical of the second (Mankiewicz, 1988). Where the community is dominated by heterotrophic organisms, especially by filter feeders, it is a signal for increased trophic resources. And when organisms adapted to oligotrophy and mesotrophy (zooxanthellate corals and calcareous algae) are missing, it usually indicates that eutrophication has occurred. Upwelling of nutrient-rich cool water and/or nutrient-enriched terrestrial runoff could be responsible for the increase in productivity and the dominance of bryomol sediments in a tropical/subtropical setting

(Moissette and Saint Martin, 1992; Gonera et al., 2000). However, McKinney and Hageman (2006) found filter-feeding epibenthic sessile invertebrates, among them bryozoans, to dominate in oligotrophic waters of the temperate northern Adriatic Sea, but decline in regions with higher nutrient levels, where endobenthic organisms prevail. Nutrient excess also increases the production of organic matter in surface waters, thus limiting oxygen supply to the seafloor and consequently the development of sessile benthic communities.

The sections of Sámsonháza, Mátraverebély and Mátraszőlős display signals of a high-productivity event. An underlying small coral reef indicates warm, (sub)tropical environment and oligotrophic sea. Both the underlying and overlaying corallinacean limestone beds indicate oligotrophic (possibly mesotrophic) conditions. Abundance of the filter-feeding bivalve *Isognomon* higher in the succession is a clear signal of elevated trophic levels (e.g., Lazareth et al., 2003), supported by a lack of photosynthetizing organisms in this layer. The laminated diatomaceous, anoxic shales in the Mátra, Börzsöny and Mecsek Mountains are the stratigraphic equivalents of the slope bryozoan limestones (Hajós, 1959, 1977; Hámor, 1970). They indicate that the high-productivity event was not local but regional in extent. The carbonate platforms in Austria also recorded repeated hypoxic events in Late Badenian time (Schmid et al., 2001).

8. Conclusion

The Badenian sedimentary deposits of Hungary yielded abundant and diverse assemblages of bryozoans (238 species) corresponding to various habitats and depositional depths: carbonate platform, terrigenous platform, slope, and basin (Fig. 7). Skeletal production and spatial distribution of carbonate factories were largely controlled by terrigenous input. Frequent shifting of facies/habitats through time and space produced a complex mosaic of environments where carbonate and siliciclastic deposits intermingled and where bryozoan communities could flourish.

Among bryozoans, nine colonial morphotypes have been recognized, with boring colonies representing a subordinate type. The relative abundance of each zoarial form has been used as a measure of the environmental conditions (water depth, water energy, sedimentation rate, and substrate types) in which a given assemblage lived. Instead of presence/absence analysis of morphotypes, we applied quantitative methods as a tool to identify similarities between samples and between localities. Quantification is based on the number of bryozoan

fragments, each of them, whatever its size, being counted as one unit. The complete data set for these numerical analyses includes 43 samples, 10 colonial morphotypes, 45 assemblages, and 238 specific taxa (+1 for unidentified celleporiforms).

The relationships between zoarial forms and environmental conditions are relatively well established, but some caution must be exercised. First, bryozoans may live cryptically within interstices and sheltered cavities of the substratum and bioconstructions where they encounter environmental conditions corresponding to deeper, quieter, habitats (Harmelin, 1988; Taylor and Wilson, 2003). In addition, depth limits in a certain region may be different in other regions due to variations in thermal regime and hydrological conditions. Finally, taphonomic and diagenetic losses may also bias the original ecological information.

As indicated by numerous marine warm-water organisms, a subtropical climate prevailed in the Central Paratethys at a time when connections with the Mediterranean were also relatively easy (Moissette et al., 2006). Nevertheless, abundant bryomol carbonates, frequently used as cool-water indicators, also occur in the same basin. The following scenario is proposed to reconcile the coeval existence of coral reefs and bryozoan–mollusc–dominated sediments. A major cause of decline in carbonate production is shadowing of photosynthetizing organisms by algal blooms. This causes a significant reduction in the depth of the euphotic zone. We suggest that bryozoan limestones were deposited below and coral reefs above the euphotic/aphotic boundary.

Acknowledgements

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