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Bryozoan faunas in the Middle Miocene of Hungary: biodiversity and biogeography

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Abstract

A study of the Badenian (Middle Miocene) marine deposits of Hungary yielded a rich bryozoan fauna of 238 species comprising 59 cyclostomes, 176 cheilostomes, and 3 ctenostomes. Six palaeobiogeographic groups have been identified among this fauna on the basis of the present-day and fossil distribution of the species. Similarities within the Central Paratethys and between the Central Paratethys, the Mediterranean and the Atlantic have then been calculated using Jaccard's index.

The results indicate strong affinities between the Central Paratethyan basins of Hungary, Austria, Poland, and Romania. The higher number of species and the lower level of endemism observed in Hungary is explained by the vicinity of this basin to the entrance of the water seaway connecting the Mediterranean to the Paratethys. A decrease in taxonomic diversity between the Early and the Late Badenian is also observed, accompanied by the absence of most tropical taxa from the Late Badenian. This points towards a less optimal climate and a more pronounced isolation of the Badenian sea from the oceanic waters.

The major result of the comparative study between Central Paratethyan and Mediterranean bryozoan faunas is the presence of numerous common species. The number of endemic Paratethyan species is however relatively high, indicating that the bryozoan faunas of both seas evolved in a relative isolation. The exchange of faunas between the Mediterranean and the Paratethys was probably regulated by an anti-estuarine circulation permitting an easier incursion of Mediterranean species into the Paratethys, but hindering the Paratethyan endemics from entering the Mediterranean. The stronger affinity between Hungarian and Mediterranean faunas also shows that this basin was closer to the entrance of the water seaway connecting the two areas and thus the Mediterranean species entered more easily.

The similarity index between Central Paratethys and Atlantic faunas is much lower than with the Mediterranean. This indicates that the palaeobiogeographic domain formed by the Mediterranean and the Paratethys was relatively homogeneous during the Middle Miocene and that the relationships with the Atlantic were weaker.

Exchange of benthic organisms between the Central Paratethys and the Indo-Pacific during the Middle Miocene is considered here as extremely improbable.

Keywords: Bryozoans; Biodiversity; Biogeography; Badenian; Middle Miocene; Central Paratethys; Hungary

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1. Introduction

During the Middle Miocene, the Central Paratethys (Fig. 1) was a complicated array of tectonic depressions housing a sea which during the entire time span of the Badenian (Langhian to Early Serravallian) retained a salinity close to oceanic, at least in most of its central, Pannonian part (Hámor, 1995). This involves the existence of at least one two-way water exchange with the world ocean system. The marine faunas of the Central Paratethys remained essentially the same during the entire Badenian (16.4 to 13.0 Ma), which points to a more or less continuous and uniform relationship with neighbouring water systems. Most presumably, the main connection of the Paratethys was with the Mediterranean Sea, through a yet unknown seaway. A number of authors (Kókay, 1985; Hámor, 1995; Rögl, 1998a,b) proposed that this connection occurred through a trough at about the confluence of the Dinaric Alps and the Alps, somewhere in the present-day Slovenia.

It is difficult to draw a reliable palaeogeographic map of the Badenian for the Hungarian part of the Central Paratethys because most of the Pannonian Basin was deeply buried and partly eroded during the Late Miocene. In addition, the palaeogeographic pattern significantly changed during the Badenian due to tectonic events (e.g. Kókay, 1985) and, without a detailed study, it is often difficult to distinguish the substages of the Badenian from each other. The distribution of Badenian sediments in Hungary thus does not reflect correctly the palaeogeography of any given time slice or instant (Fig. 2).

Although their presence and abundance is often mentioned in geological and palaeontological papers (partly published in Hungarian), the Badenian bryozoans of Hungary have practically never been studied. As this paper reveals, they are however abundant and diverse in various marine deposits: biohermal limestones, biocalcarenites, sandstones, and marls. The 85 samples collected at 18 localities (outcrops and cores), complemented with some museum specimens, yielded a total of 238 species. Most species lived in shallow- to moderately deep-water environments and the occurrence of abundant warm-water taxa, together with the presence of coral patch reefs in the same basins, indicates a subtropical to tropical climate (Saint Martin et al., 2000).

The studied bryozoans have been classified into six biogeographic groups: Eastern Atlantic/Mediterranean, Mediterranean, Paratethyan endemics, cosmopolitan, and Indo-Pacific. The sixth group comprises species of unknown or dubious affinities. The relationships between the Central Paratethyan bryozoan faunas have been analysed. A comparison of the Paratethyan

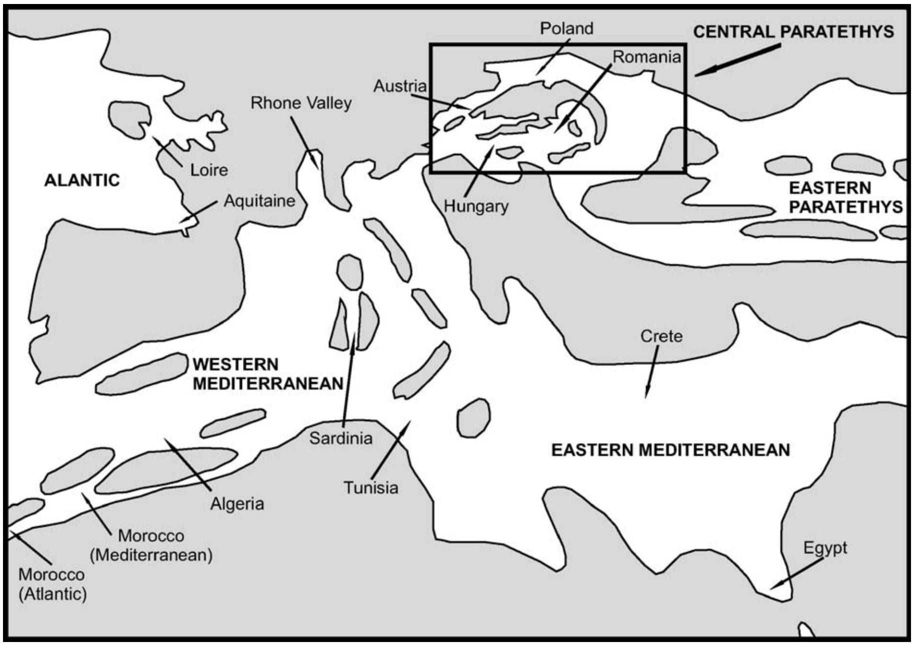

Fig. 1. Map of the Central Paratethys, the Mediterranean, and the Eastern Atlantic basins during the largest extension of the Paratethys in Early Badenian time (modified from Alvinerie et al., 1992; Rögl, 1998b; Popov et al., 2004). Arrows indicate the approximate location of the sedimentary basins where bryozoan faunas have been studied.

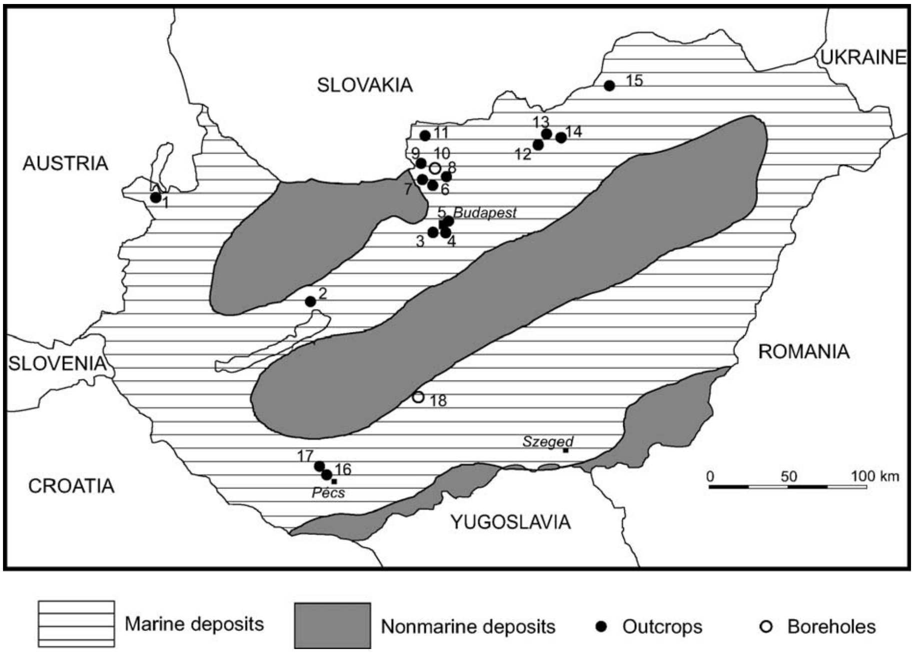

Fig. 2. Map of Hungary showing the distribution of marine deposits during Badenian times and the location of sampling sites (modified from Nagymarosy and Müller, 1988; Hámor, 1995). Numbers correspond to studied localities and cores: (1) Fertőrákos, (2) Várpalota, (3) Diósd, (4) Budapest-Rákos, (5) Budapest-Őrsvezér tere, (6) Visegrád, (7) Zebegény, (8) Törökmező, (9) Szob, (10) Szokolya-2, (11) Kemence, (12) Mátraverebély, (13) Sámsonháza, (14) Mátraszőllős, (15) Borsodbóta, (16) Kishajmás, (17) Kovácsszénájai tó, (18) Tengelic-2.

faunas with Mediterranean, Atlantic, and Indo-Pacific faunas was subsequently made.

2. Stratigraphy of the Badenian of the Central Paratethys

Attempts at stratigraphical subdivision of the Badenian stage (by then erroneously correlated with the Tortonian) were initiated for the Vienna Basin in the second half of the 20th century (Papp et al., 1978). This subdivision was based on benthic foraminifers. In the 1970s, an international team designated a threefold subdivision (Moravian, Wieliczian, and Kosovian), defined by stratotypes and boundary stratotypes and correlated to planktonic foraminifer and nannoplankton global zones. Kókay (1985) used this scheme and observed its good correlation with changes in the marine mollusc faunas.

This threefold subdivision of the Badenian apparently correlates well with global climatic and eustatic changes, although studies in this respect are preliminary. The Early Badenian, at least partly, seems to correspond to a climatic peak when coral reefs made their northernmost Neogene excursion to what is now southern Poland (Pisera, 1996). The Middle Badenian (Wieliczian) may correspond to a global eustatic lowstand, resulting in the cutting off of some intra- and extra-Carpathian basins and in the formation of evaporites in the Czech Republic, Poland, Romania, Slovakia, and Ukraine (e.g. Kókay, 1985; Eastoe and Peryt, 1999; Peryt, 2001; Cendón et al., 2004). The Late Badenian corresponds again to a climatic optimum with coral patch reefs in Hungary and neighbouring countries (Pisera, 1996; Saint Martin et al., 2000). In contrast to the Early Badenian examples, these reefs are however impoverished in hermatypic forms. This may point to a less optimal climate than that of the Early Badenian and/or to slight changes in salinity due to a more pronounced isolation of the Badenian Sea from oceanic waters. The last short interval ("Verarmungszone"="impoverishment zone") seems to indicate the almost complete isolation from the Mediterranean and an increasing exchange of water and faunas with the by then brackish Eastern Paratethys (Kókay, 1985).

Although this threefold system is by and large a good working base, quite often there are correlation problems, especially in shallow-water deposits lacking planktonic elements. Moreover, the subdivision of the Badenian stage into three substages is based on stratotypes established in very different parts of the Paratethys and the boundaries between them are often controversial. As a consequence, some authors prefer to use a twofold subdivision (Pisera, 1996; Vakarcs et al., 1998; Jimenez-Moreno et al., 2005) and this is also the option chosen throughout this paper.

3. Study materials and methods

Most of the material used in this study (59 samples taken from 16 sections or isolated outcrops) was collected by the authors during field excursions in 1996, 1997, 2000, and 2001 (Fig. 2).

The Hungarian Geological Survey realized in the 1950s and 1960s a great effort of coring over the whole Hungarian territory. We were able to sample the Badenian interval of one of the cores (Tengelic-2) made in predominantly argillaceous sediment (25 samples, but only 8 containing bryozoans). Another core (Szokolya-2) also yielded some bryozoans in 18 samples (Fig. 2).

Material from the Hungarian Natural History Museum (Department of Geology and Palaeontology, Budapest) was also used to complement the biodiversity aspect of this study. Most museum specimens came from outcrops we ourselves sampled, but in some cases this material helped us find unknown or poorly explored fossil deposits. Well-preserved museum specimens were also used for an easier identification of some species and SEM study for a future monograph on the Hungarian Badenian bryozoan faunas.

In order to analyse the relationships between the bryozoan faunas from the Badenian of Hungary, the Badenian of other Central Paratethyan basins, and the Mediterranean and Atlantic Miocene, we compiled from published material a systematic database. After a revision of some of the names to ensure systematic coherence, we obtained a list of 682 species. A binary similarity coefficient, based on presence/absence of species, was then calculated to compare the different faunas. Jaccard's Coefficient of Community (Jaccard, 1901) was chosen because it performs better than most others in palaeoecology and palaeobiogeography (Shi, 1993). This similarity index is calculated as: $C/(A+B-C)$, where C is the number of species present in both samples, A is the total number of species in sample 1, and B the total number of species in sample 2. For easier handling, the calculated values have been multiplied by 100 and the results corrected to the nearest whole number.

The six (palaeo)biogeographic groups used in this study have been defined on the basis of the published present-day and fossil distributions of the bryozoan species. They are based on the location of previous monographic studies and on units commonly accepted in palaeo- and biogeography (e.g. Marinescu, 1992; Westermann, 2000; Harzhauser et al., 2002; Meulenkamp and Sissingh, 2003). The four sedimentary basins under consideration have been termed herein informally Austria (Vienna and Styrian Basins), Hungary (Pannonian Basin), Poland (Carpathian Foredeep), and Romania (Transylvanian Basin).

4. Palaeobiodiversity

A total of 238 bryozoan species were identified among the collected material: 176 cheilostomes, 59 cyclostomes, and 3 (boring) ctenostomes (Tables 1–6). Some of the species left in open nomenclature may be new to science; this is especially the case for *Goodonia* sp., *Alysidotella* sp., *Buskea* sp., and *Smittina* sp.

A fairly large number of extant or fossil species are reported here for the first time from the Paratethys. Among them, the most common are the following: *Annectocyma major*, *Callopora dumerili*, *Catenicella elegans*, *Cheiloporina campanulata*, *Schedocleidochasma porcellanum*, *Copidozoum tenuirostre*, *Cosciniopsis ambita*, *Cribrilina messiniensis*, *Distansescharella seguenzai*, *Electra monostachys*, *Ellisina gautieri*, *Escharella peachi*, *Escharella reussiana*, *Fenestrulina harmelini*, *Gemellipora eburnea*, *Herentia musensis*, *Hippothoa flagellum*, *Lagenipora lepralioides*, *Omalosecosa ramulosa*, *Pentapora fascialis*, *Plagioecia platydiscus*, *Plagioecia sarniensis*, *Puellina gigantea*, *Reptomulticava parviporosa*, *Reussia elongata*, *Savignyella lafonti*, *Schizomavella discoidea*, *Smittina canavarii*, *Steginoporella intermedia*, *Tetrocycloecia dichotoma*, and *Tubulipora plumosa*. In addition, a very few ctenostome bryozoans had previously been reported in the literature from the Paratethys (Baluk and Radwanski, 1979).

Comparably high taxonomic diversities have also been noted in other Badenian basins of the Central Paratethys: 185 species in Austria (Reuss, 1848, 1874; Manzoni, 1877; David and Pouyet, 1974; Vávra, 1974, 1975, 1979a,b, 1989; Schmid, 1989), 191 species in Poland (Malecki, 1949, 1952, 1976, 1978; Pouyet, 1997; Pouyet and Tarkowski, 1998), and 187 species in Romania (Ghiurca, 1961, 1966, 1971, 1972, 1974; Nicorici, 1961; Ghiurca and Nicorici, 1963; Ghiurca and Clichici, 1972; Ghiurca and Gábos, 1973; Ghiurca and Baluta, 1977; Ghiurca and Florei, 1980). The species richness of the Hungarian bryozoan faunas is however higher, especially if we take into account that this paper constitutes practically the first study to date of this group in the Hungarian Miocene and that relatively few samples (85, but some of them yielding only scarce colony fragments) were studied.

A comparison with the Mediterranean Early Miocene bryozoan faunas of the Rhone valley of France

(David et al., 1970, 1972; Li, 1990; Pouyet, 1991), the Middle Miocene of Egypt (Souaya, 1965; Ziko, 1994; Ziko et al., 1994; El Safori, 2000, 2002), and the Late Miocene of Algeria (Moissette, 1988, 1993) and Morocco (El Hajjaji, 1992; Moissette and Saint Martin, 1995) shows comparable biodiversities: 183 species in the Rhone Valley, 167 in Egypt, 185 in Algeria, and 215 in Morocco. The bryozoan faunas of Tunisia (Burdigalian-Langhian: Blondel et al., 1990), Sardinia (Langhian-Serravallian: Annoscia, 1967), Crete (Tortonian-Messinian: Moissette et al., 1993), and Tunisia (Messinian: Moissette, 1997) have been less well studied and far fewer species are known from these regions: 51, 47, 49, 104, and 29, respectively.

The Miocene bryozoan faunas of the eastern Atlantic are also rich in species. The better studied are those from two basins of western France. A total of 171 and 85 species respectively have thus been described from the Early and Middle Miocene of the Aquitaine Basin (Vigneaux, 1949 and references therein). With 260 species, the Middle Miocene faunas of the Loire Valley (Buge, 1957 and references therein) are still more diverse. Far fewer species (77) are known from the Late Miocene of Atlantic Morocco (Sefian et al., 1999).

From a palaeoclimatic point of view, most of the species identified in the Badenian of Hungary are temperate or warm-temperate. However, the tropical taxa (species or genera, underlined in Tables 1–5) are relatively numerous (20) and some of them are even abundant in a number of samples (e.g. *Metrarabdotos maleckii*, *Steginoporella* spp., and *Tremopora radicifera*). On the contrary, the cold-water (boreal) species (e.g. *Palmicellaria skenei* and *Amphiblestrum trifolium*) are not diverse and are always rare in the studied assemblages.

An analysis of the temporal distribution of the Badenian bryozoans of Hungary reveals that 110 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. This decrease in diversity is accompanied by the conspicuous absence of most tropical taxa from the Late Badenian sediments. As previously mentioned, a similar impoverishment is observed in hermatypic corals. This may indicate a less optimal climate or a more pronounced isolation of the Badenian sea from the oceanic waters leading to slight changes in salinity (Müller, 1984; Pisera, 1996).

5. Palaeobiogeography

Apart from the other Badenian Central Paratethys basins, the bryozoan faunas of the Mediterranean and the Eastern Atlantic have been the object of numerous publications either from the fossil (see references above) or the Recent (Gautier, 1962; Prenant and Bobin, 1966; Hayward, 1974; Harmelin, 1976, 1977; Ryland and Hayward, 1977; Harmelin and d'Hondt, 1982; Hayward and Ryland, 1985; Zabala, 1986; Zabala and Maluquer, 1988; Harmelin and d'Hondt, 1992a,b, 1993; Hayward and Ryland, 1998, 1999; Hayward and McKinney, 2002).

On the basis of their present-day and fossil distributions, the 238 species of bryozoans identified in the Badenian of Hungary have been distributed into six (palaeo)biogeographical groups.

5.1. Eastern Atlantic/Mediterranean species

This group is by far the most abundant (73 species, 31%). It comprises species with a Recent and/or fossil distribution from northern Morocco and Madeira to the British Isles (Table 1). These species also occur in the Mediterranean, many in the Eastern Mediterranean (Harmelin, 1969; Hayward, 1974), and obviously entered the Paratethys through the Mediterranean.

Several species also occurring in the present-day Atlantic lived during the Middle Miocene only in the Mediterranean–Paratethys realm and later (from the Late Miocene to the Pleistocene) only in the Mediterranean. Most of these species are rare in the Atlantic today and probably constitute recent introductions from the Mediterranean. Examples of this group are notably: *Adeonella polystomella*, *Frondipora verrucosa*, *Hagiosynodos latus*, *Plagioecia platydiscus*, *Schizoporella longirostris*, *Schizotheca fissa*, *Steraechmella buski*, and *Turbicellepora coronopus*.

5.2. Endemic Mediterranean species

Relatively numerous, these 55 species (23%) have a Recent and/or fossil distribution limited to the Mediterranean (Table 2). They may correspond to relics of Tethyan faunas, or they may have evolved in situ from immigrants of Atlantic or Indo-Pacific origin.

The occurrence and abundance of these species, together with those of the Eastern Atlantic/Mediterranean group (totalling 128 species = 54%), clearly indicate that there was during the Middle Miocene a community of faunas in this palaeogeographic region (Fig. 1).

5.3. Endemic Paratethyan species

This group is made up of 50 species (21%) never recorded outside the Central Paratethys (Table 3). Until

Table 1
List of the Eastern Atlantic/Mediterranean bryozoan species represented in the Badenian of Hungary

*Adeonella polystomella** (Reuss, 1848)	*Omalosecosa ramulosa** (Linnaeus, 1767)
Amphiblestrum aff. *trifolium** (Wood, 1844)	*Onychocella angulosa** (Reuss, 1848)
*Buffonellaria divergens** (Smitt, 1873)	*Orbignyopora archiaci** (Fischer, 1866)
Buffonellodes incisa (Reuss, 1874)	*Palmiskenea skenei** (Ellis and Solander, 1786)
*Callopora dumerili** (Audouin, 1826)	*Patinella radiata** (Audouin, 1826)
*Calloporina decorata** (Reuss, 1848)	*Pentapora fascialis** (Pallas, 1766)
*Calpensia nobilis** (Esper, 1796)	*Plagioecia platydiscus** Harmelin, 1976
*Cellaria salicornioides** Lamouroux, 1816	*Reptomulticava parviporosa*? Canu and Lecointre, 1934
Cellepora "*pumicosa*"* (Waters, 1879)	*Reteporella beaniana** (King, 1846)
Celleporaria cerioporoides (Canu and Lecointre, 1930)	*Reteporella cellulosa** (Linnaeus, 1767)
Celleporaria palmata (Michelin, 1847)	*Reussirella haidingeri* (Reuss, 1848)
Celleporina aff. *lucida** (Hincks, 1880)	*Rosseliana incompta* (Reuss, 1874)
Ceriopora tumulifera? (Canu and Lecointre, 1934)	*Schizobrachiella sanguinea** (Norman, 1868)
Crisia lecointrei Bobies, 1958	*Schizomavella auriculata** (Hassall, 1842)
Desmeplagioecia tenuis? (Reuss, 1869)	*Schizomavella* aff. *discoidea** (Busk, 1859)
Disporella grignonensis? (Milne Edwards, 1838)	*Schizoporella dunkeri** (Reuss, 1848)
*Electra monostachys** (Busk, 1854)	*Schizoporella longirostris** Hincks, 1886
Entalophoroecia gracilis?* Harmelin, 1976	*Schizoporella unicornis** (Johnston, 1847)
Entalophoroecia robusta?* Harmelin, 1976	*Schizotheca fissa** (Busk, 1856)
*Escharella peachi** (Johnston, 1847)	*Scrupocellaria elliptica* (Reuss, 1848)
Escharella reussiana (Busk, 1859)	*Smittina cervicornis** (Pallas, 1766)
*Escharella variolosa** (Johnston, 1838)	*Smittina* cf. *colleti** (Jullien, 1903)
*Escharina vulgaris** (Moll, 1803)	*Steginoporella intermedia* Buge and David, 1967
*Escharoides coccinea** (Abildgaard, 1806)	*Steraechmella buski** Lagaaij, 1952
*Frondipora verrucosa** (Lamouroux, 1821)	*Thalamoporella neogenica* Buge, 1950
*Hagiosynodos latus** (Busk, 1856)	*Tremopora radicifera** (Hincks, 1881)
Hemicyclopora collarina Canu and Lecointre, 1925	*Tetrocycloecia dichotoma* (Goldfuss, 1827)
*Herentia hyndmanni** (Johnston, 1847)	*Trypostega rugulosa* (Reuss, 1874)
*Hincksina flustroides** (Hincks, 1877)	*Tubulipora dimidiata* (Reuss, 1848)
Hippoporella bicornis Canu and Lecointre, 1928	*Tubulipora flabellaris*?* (Fabricius, 1780)
*Hippothoa flagellum** (Manzoni, 1870)	*Tubulipora plumosa*?* Harmer, 1898
*Hornera frondiculata** Lamouroux, 1821	*Turbicellepora canaliculata*?* (Busk, 1886)
Hornera lichenoides?* (Linnaeus, 1758)	*Turbicellepora coarcta* (Canu and Lecointre, 1930)
*Lagenipora lepralioides** (Norman, 1868)	*Turbicellepora* cf. *compressa** (Busk, 1859)
Lunulites androsaces Michelotti, 1838	*Turbicellepora coronopus** (Wood, 1844)
Mesenteripora meandrina (Wood, 1844)	*Ybselosoecia typica* (Manzoni, 1878)
Micropora parvicella Canu and Lecointre, 1927	

Extant species are indicated by an asterisk and tropical taxa are underlined.

proven otherwise, these species are considered as endemic to the Paratethys. The decrease in bryozoan diversity is particularly strong for this palaeobiogeographic group, with a drop of about 34% between the Early and the Late Badenian of Hungary.

With the exception of a very small number of euryhaline species surviving until the Sarmatian (Late Serravallian), almost all bryozoans disappeared from the Paratethys (Ghiurca and Stancu, 1974) at the end of the Badenian when marine connections were interrupted and the Paratethys became a brackish sea.

5.4. Cosmopolitan species

Thirty species (13%) can be considered as cosmopolitan (Table 4). They have a vast geographic distribution (generally with the exception of polar seas): Mediterranean, both sides of the Atlantic Ocean and often Indian and Pacific Oceans. All these species are extant, generally ranging from at least the Early Miocene.

5.5. Indo-Pacific species

This group comprises a small number of species (10=4%) with Indo-Pacific affinities (Table 5). As noted by Hayward (1974), the similarity between the Mediterranean and the Indo-Pacific is more likely to be found when taking into account the distribution of genera instead of species. This is the case with mostly Indo-Pacific genera such as *Arachnopusia*, *Cosciniopsis*, *Emballotheca*, *Hippaliosina*, *Margaretta*, and *Polyascosoecia* (Vávra, 1980). They are

Table 2
List of the endemic Mediterranean bryozoan species represented in the Badenian of Hungary

Annectocyma echinata (Münster *in* Goldfuss, 1826)	*Hornera subannulata* Philippi, 1843
Aplousina bobiesi (David and Pouyet, 1974)	*Membraniporella ungeri* (Reuss, 1848)
Batopora rosula (Reuss, 1848)	*Micropora papyracea* (Reuss, 1848)
Callopora fenestrata (Reuss, 1848)	*Multigalea* (?) sp.
Calpensia gracilis (Münster, 1826)	*Myriapora truncata** (Pallas, 1766)
Canda rectangulata Udin, 1964	*Patinella goldfussi* (Reuss, 1864)
Cellepora globularis Bronn, 1837	*Patinella mediterranea* de Blainville, 1834
Cheiloporina campanulata (Cipolla, 1921)	*Patinella prolifera* (Reuss, 1848)
Crassimarginatella diadema (Reuss, 1848)	*Pleuronea pertusa* (Reuss, 1848)
Crassimarginatella macrostoma (Reuss, 1848)	*Porella cheilopora* (Reuss, 1848)
Cribellopora latigastra (David, 1949)	*Porella erecta*? David, Mongereau and Pouyet, 1972
Cribrilaria rarecostata (Reuss, 1848)	*Pseudofrondipora davidi* Mongereau, 1970
Cribrilina messiniensis Pouyet and Moissette, 1986	*Puellina gigantea* David, Mongereau and Pouyet, 1972
Crisia haueri (Reuss, 1848)	*Ramphonotus appendiculata* (Reuss, 1848)
Crisia hoernesi Reuss, 1848	*Reussia elongata* (David, Mongereau and Pouyet, 1972)
*Distansescharella seguenzai** Cipolla, 1921	*Rhagasostoma stenostoma* (Reuss, 1848)
*Ellisina gautieri** Fernandez Pulpeiro and Reverter Gil, 1993	*Schismoporella schizogaster* (Reuss, 1848)
Escharella tenera (Reuss, 1874)	*Schizoporella geminipora* (Reuss, 1848)
Escharoides megalota (Reuss, 1848)	*Schizoporella tetragona* (Reuss, 1848)
Fenestrulina harmelini David and Pouyet, 1972	*Schizostomella grinzingensis* David and Pouyet, 1974
Goodonia sp.	*Smittina canavarii* (Neviani, 1900)
Herentia musensis (David and Pouyet, 1976)	*Steginoporella cucullata* (Reuss, 1848)
Hinksina loxopora (Reuss, 1848)	*Trochiliopora beyrichi* (Reuss, 1851)
Hippadenella regularis (Reuss, 1874)	*Tubulipora foliacea* Reuss, 1848
Hippopleurifera hypsostoma (Reuss, 1874)	*Turbicellepora crenulata*?* Hayward, 1978
Hippopleurifera semicristata (Reuss, 1848)	*Umbonula monoceros* (Reuss, 1848)
Hippoporella pauper (Reuss, 1874)	*Watersipora goniostoma* (Reuss, 1848)
Hippoporina rarepunctata (Reuss, 1848)	

Extant species are indicated by an asterisk and tropical taxa are underlined.

Table 3
List of the endemic Paratethyan bryozoan species represented in the Badenian of Hungary

Alderina nobilis (Reuss, 1848)	*Idmidronea disticha* (Reuss, 1848)
Bobiesipora fasciculata (Reuss, 1848)	*Iodictyum rubeschi* (Reuss, 1848)
Celleporaria foraminosa (Reuss, 1848)	*Lacerna fuchsi* (Reuss, 1874)
Celleporina bugei Pouyet, 1973	*Metrarabdotos maleckii* Cheetham, 1968
Celleporina minuscula Pouyet, 1973	*Microporella inamoena* (Reuss, 1874)
Coleopora insignis (Reuss, 1874)	*Oncousoecia biloba* (Reuss, 1848)
Cribella cyclocephala (Reuss, 1874)	*Patinella stellata* (Goldfuss, 1826)
Crisidmonea foraminosa (Reuss, 1851)	*Phylactella uniserialis* (Canu and Bassler, 1925)
Cupuladria vindobonensis Baluk and Radwanski, 1984	*Plagioecia rotula* (Reuss, 1848)
Ellisina grandis? Canu and Bassler, 1925	*Puellina kollmanni* (David and Pouyet, 1974)
Entalophoroecia anomala (Reuss, 1848)	*Saevitella inermis*? Bobies, 1956
Entalophoroecia clavula (Reuss, 1848)	*Schizomavella grossipora* (Reuss, 1874)
Entalophoroecia fasciculifera (Canu and Bassler, 1923)	*Schizomavella tenella* (Reuss, 1848)
Entalophoroecia pulchella (Reuss, 1848)	*Smittipora platystoma* (Reuss, 1848)
Escharella arrecta (Reuss, 1848)	*Steginoporella reussi* David and Pouyet, 1972
Escharella circumornata (Reuss, 1848)	*Steginoporella tuberculata margarittae* David and Pouyet, 1979
Escharina polyomma (Reuss, 1848)	*Stomatopora subdivaricata* (d'Orbigny, 1852)
Figularia haueri (Reuss, 1848)	*Tremogasterina areolata* (Reuss, 1874)
Figularia manzonii (Reuss, 1874)	*Tubulipora partschi* (Reuss, 1848)
Hincksipora porosa? (Manzoni, 1877)	*Tubulipora pluma* (Reuss, 1848)
Hippopleurifera ampla (Reuss, 1848)	*Turbicellepora aviculifera* (Manzoni, 1877)
Hippopleurifera aperta (Reuss, 1874)	*Turbicellepora krahuletzi*? (Kuhn, 1925)
Hippopleurifera biauriculata (Reuss, 1848)	*Umbonula austriensis*? David and Pouyet, 1974
Hippopleurifera binata? (Reuss, 1874)	*Umbonula macrocheila* (Reuss, 1848)
Hippoporina sulcifera (Reuss, 1874)	*Vibracella trapezoidea* (Reuss, 1848)

Tropical taxa are underlined.

Table 4
List of the cosmopolitan bryozoan species represented in the Badenian of Hungary

*Aetea sica** (Couch, 1844)	*Diplosolen obelium** (Johnston, 1838)
*Annectocyma major** (Johnston, 1847)	*Disporella hispida** (Fleming, 1828)
Antropora cf. *granulifera** (Hincks, 1880)	*Escharina dutertrei** (Audouin, 1826)
*Biflustra savarti** (Audouin, 1826)	*Gemellipora eburnea** Smitt, 1873
*Catenicella elegans** Busk, 1852	*Idmidronea atlantica** (Forbes in Johnston, 1847)
*Cellaria fistulosa** (Linnaeus, 1758)	*Microporella ciliata** (Pallas, 1766)
*Schedocleidochasma porcellanum** (Busk, 1860)	*Mollia patellaria** (Moll, 1803)
*Chorizopora brongniarti** (Audouin, 1826)	*Nellia oculata** Busk, 1852
*Conopeum reticulum** (Linnaeus, 1767)	*Plagioecia patina** (Lamarck, 1816)
*Copidozoum tenuirostre** (Hincks, 1880)	*Plagioecia sarniensis** (Norman, 1864)
*Cribrilaria innominata** (Couch, 1844)	*Reptadeonella violacea** (Johnston, 1847)
*Crisia denticulata** (Lamarck, 1816)	*Savignyella lafonti** (Audouin, 1826)
*Crisia eburnea** (Linnaeus, 1758)	*Scrupocellaria bertholleti*?* (Audouin, 1826)
*Crisia elongata** Milne Edwards, 1838	*Smittoidea reticulata** (Mac Gillivray, 1842)
*Cryptosula pallasiana** (Moll, 1803)	*Tervia irregularis** (Meneghini, 1845)

Extant species are indicated by an asterisk and tropical taxa are underlined.

considered as relics from a time when the Mediterranean (and the Paratethys) was connected to the Indian Ocean (until the end of the Early Miocene).

However, several authors (Marinescu, 1992; Rögl, 1998b, 1999) still argue that connections existed during the Middle Miocene (Early and Late Badenian) between the Paratethys and the Indo-Pacific. The existence of these seaways has been suggested by the occurrence in Austrian and Romanian Basins of several groups of planktonic and nektonic organisms with Indo-Pacific affinities: nannoplankton, diatoms, radiolarians, pteropods, and fishes (Dumitrica et al., 1975; Rögl and Müller, 1976; Popescu, 1979). Nevertheless, and at least on the basis of the bryozoan faunas, exchange of benthic organisms between the two regions is considered as extremely improbable.

5.6. Species of unknown or dubious origin

The remainder of the identified species have been put in this group because they were left in open nomenclature and from lack of knowledge about the origin of the corresponding genera (Table 6). Their number and proportion are relatively low (20 species, 8%). No precise palaeobiogeographic significance is attached to this group.

6. Comparison between Badenian bryozoan faunas of the Central Paratethys

A comparison with the other Central Paratethys faunas was undertaken on the basis of works previously published by several authors about bryozoans from Austria, Poland, and Romania (see references above). No Badenian bryozoan faunas are known from the Eastern Paratethys and our comparison is thus limited to the Central Paratethys.

A relatively high number of species (64) have been recorded from all four basins: only seven of these are endemic to the Paratethys, whereas the others also occur in the Atlantic and/or the Mediterranean. A number of species (59) have been found in three different basins (20 are endemic) and a greater sampling effort would probably prove that many of these are in fact common to all four basins. Eighty-two species (among them 37 endemics) were recorded from two basins and 179 species (63 endemic) from only one basin. This means that, among the 384 bryozoan species of the Central Paratethys, 127 are endemics (33%).

Noticeable is the variation in number (and percentage) of Paratethyan endemic species within the Central Paratethys: 50 (21%) in Hungary, 51 (27%) in Poland, 67 (36%) in Austria, and 80 in Romania (43%). The

Table 5
List of the Indo-Pacific bryozoan species represented in the Badenian of Hungary

Arachnopusia sp.	*Hippaliosina depressa** (Busk, 1852)
*Celleporina costazi** (Audouin, 1826)	*Margaretta cereoides** (Ellis and Solander, 1786)
*Cosciniopsis ambita** Hayward, 1974	*Monoporella nodulifera** (Hincks, 1881)
Crepidacantha odontostoma (Reuss, 1874)	*Polyascosoecia coronopus* (Canu and Bassler, 1922)
Emballotheca longidens (Cipolla, 1921)	*Stenosipora simplex* (Koschinsky, 1885)

Extant species are indicated by an asterisk and tropical taxa are underlined.

Table 6
List of the bryozoan species of uncertain or unknown origin represented in the Badenian of Hungary

Alysidotella sp.	*Plagioecia* sp.
Buskea sp.	*Prenantia* sp.
Cupuladria sp.	*Schizoporella* sp.
Entalophoroecia sp.	*Scrupocellaria* sp.
Heteropora sp.	*Smittina* sp.
Hippodiplosia sp.	*Spathipora* sp.
Hippopleurifera sp.	*Terebripora* sp.
Membraniporidra sp.	*Tubulipora* sp. 1
Metroperiella sp.	*Tubulipora* sp. 2
Perigastrella sp.	*Turbicellepora* sp.

low level of endemism observed in the Badenian of Hungary is best explained by the vicinity of this basin to the entrance of the water seaway connecting the Mediterranean to the Paratethys (in the Dinarides) and thus an easier influx of Mediterranean and Atlantic/Mediterranean species. Austria, which is also close to this seaway, has however a relatively high number of endemic species. A possible explanation for this observation is that landmasses or islands (as shown on Fig. 3) may have hindered the introduction of Mediterranean species by currents into the western part of the Central Paratethys.

The biogeographical relationships between the basins of the Central Paratethys are indicated on Fig. 3. With values of Jaccard's index of 30 to 50 (average 38), the faunal similarities are high and this indicates that a stock of common species existed throughout the Central Paratethys during the Badenian. The lowest values are between Romania and the other basins (30–35), suggesting that this region remained relatively more isolated.

The Paratethyan endemic species originated from in situ evolution of taxa since the Late Eocene–Early Oligocene when the Tethys Ocean vanished, giving rise to the Paratethys and the Mediterranean Seas (Rögl, 1998a,b, 1999; Meulenkamp and Sissingh, 2003).

7. Comparison between Miocene Paratethys, Mediterranean, and Atlantic bryozoan faunas

Mediterranean bryozoan faunas coeval with those of the Central Paratethys are relatively rare or poorly known: Langhian-Serravallian of Egypt (Souaya, 1965; Ziko, 1994; Ziko et al., 1994; El Safori, 2000, 2002) and Sardinia (Annoscia, 1967), and Late Burdigalian–Late Langhian of Tunisia (Blondel et al., 1990). Our comparison with other Miocene bryozoan faunas thus concentrates on the Early Miocene (Burdigalian) of France (Rhone valley: David et al., 1970, 1972; Li, 1990; Pouyet, 1991) and the Late Miocene (mostly Messinian) of Algeria (Moissette, 1988, 1993), Morocco (El Hajjaji, 1992; Moissette and Saint Martin, 1995), Sardinia (Moissette, personal data), Crete (Moissette et al., 1993), and Tunisia (Moissette, 1997). The slow evolution of bryozoans diminishes the importance of the time factor when evaluating relationships between the Paratethys and the Mediterranean.

The major result of the comparative study between Central Paratethyan and Mediterranean faunas (384 and

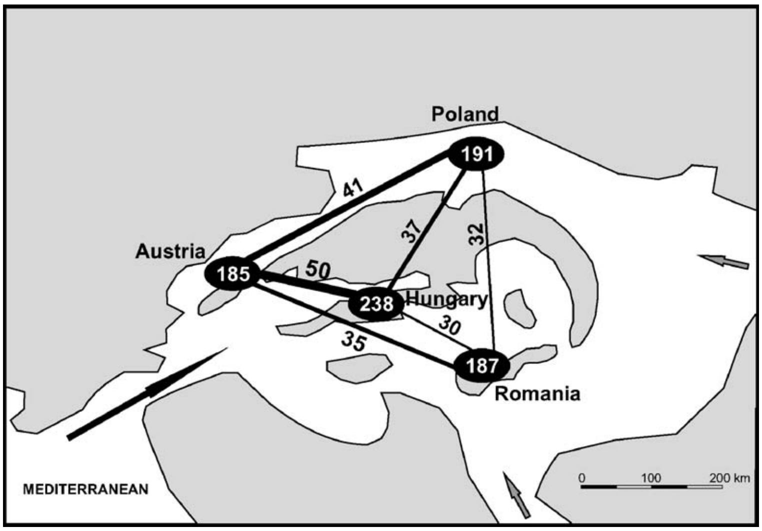

Fig. 3. Palaeobiogeographic relationships between bryozoan faunas, indicated by values of Jaccard's index, for the various basins of the Central Paratethys (map modified from Rögl, 1998a). Numbers in black ovals are values of species richness. Arrows represent the main possible currents entering the Central Paratethys basin, either from the Eastern Paratethys (small grey arrows) or from the Mediterranean (large black arrow).

468 species, respectively) is the presence of numerous common species (183). As mentioned before, the number of endemic Paratethyan species (127 = 33%) is however relatively high, indicating that the bryozoan faunas of both seas evolved in a relative isolation.

The average Jaccard's index between the Hungarian faunas and those of the Mediterranean is 23 (extreme values: 13–30) (Fig. 4). This number corresponds exactly with the average similarity value obtained when comparing the various Mediterranean faunas: 23 (range: 14–58). The average value of Jaccard's index between the other Central Paratethyan basins and the Mediterranean is only 18 (extreme values: 17–19). The stronger affinity between Hungarian and Mediterranean faunas shows a clear relationship with the palaeogeographical setting: this basin was closer to the entrance of the water seaway connecting the two areas and thus the Mediterranean species entered more easily.

A list of 461 bryozoan species from the Miocene of the Eastern Atlantic was also compiled: Early and Middle Miocene of Aquitaine (Vigneaux, 1949), Middle Miocene of Touraine (Buge, 1957), and Late Miocene of Morocco (Sefian et al., 1999). With extreme values of 9 to 16 and an average of 12, the similarity index between Paratethys and Atlantic faunas is much lower than with the Mediterranean. The figures for the comparison between Hungarian and Atlantic faunas are also low (average 13), but even more variable: 7–19 (Fig. 4). An average similarity of 13 is also obtained when comparing Mediterranean and Atlantic faunas. These observations tend to indicate that the Tethys (Mediterranean + Paratethys) constituted a relatively homogeneous palaeobiogeographic domain during the Middle Miocene and that the relationships with the Atlantic were weaker.

8. Conclusions

The Badenian bryozoan faunas of Hungary and the other basins of the Central Paratethys are very rich in species: 238 in Hungary, 185 in Austria, 191 in Poland, and 187 in Romania. The high diversity of Middle Miocene bryozoans is also in marked contrast to the much poorer faunas of the Early Miocene of Austria (Kühn, 1925; Vávra, 1975, 1979b, 1987; Schmid, 2002) and Hungary (our preliminary study).

The higher species richness of the Hungarian faunas during the Badenian is explained mostly by easier connections with the Mediterranean through the Dinarides seaway. As noted before, almost all bryozoans disappeared from the Central Paratethys at the end of the Badenian (Ghiurca and Stancu, 1974). A profound tectonic reorganization took place in the region between the Alps, the Dinarides, and the Pannonian Basin during the late Middle Miocene, thus terminating all marine connections between the Mediterranean and the

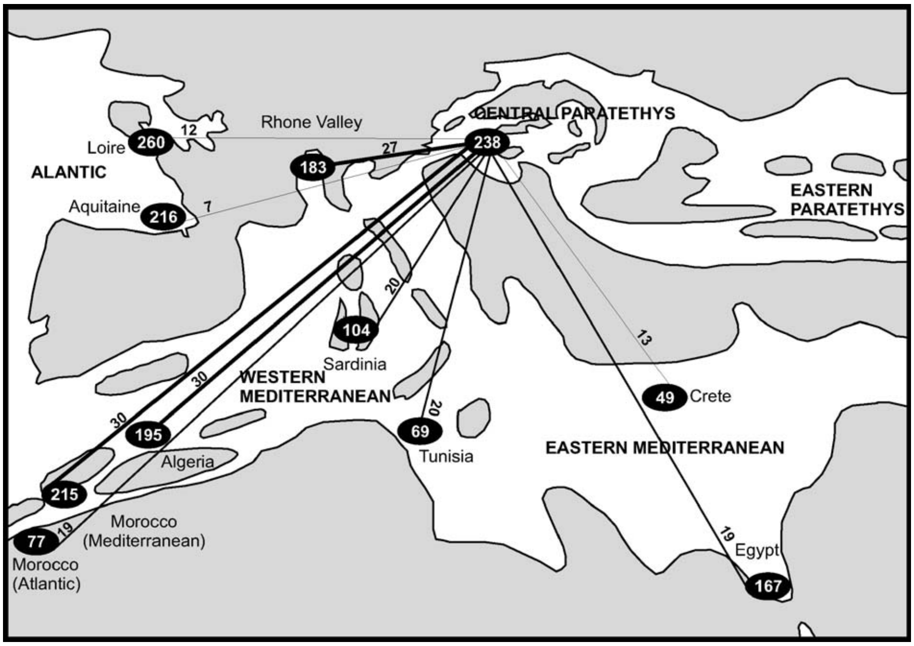

Fig. 4. Palaeobiogeographic relationships between bryozoan faunas, indicated by values of Jaccard's index, for the Hungarian basin, the Mediterranean Sea and the Eastern Atlantic basins (map modified from Alvinerie et al., 1992; Rögl, 1998b; Popov et al., 2004). Numbers in black ovals are values of species richness.

Central Paratethys (Royden and Báldi, 1988; Tomljenović and Csontos, 2001; Kuhlemann et al., 2002; Mantovani et al., 2002; Meulenkamp and Sissingh, 2003). Notwithstanding, ephemeral marine incursions from the Mediterranean into the Eastern Paratethys still occurred during the latest Middle Miocene and the Late Miocene (Rögl, 1998b, 1999; Meulenkamp and Sissingh, 2003).

During the Badenian, palaeogeographic and climatic changes, unstable salinity and low sea level caused extinctions within the Central Paratethys (e.g. Pisera, 1996; Rögl, 1999; Harzhauser and Kowalke, 2004; Janz and Vennemann, 2005). These are reflected in a decreased diversity of the Late Badenian bryozoan biota, especially in the reduced number of warm-water taxa. Similar conclusions have been made for other groups of Paratethyan marine organisms: dinoflagellates (Jimenez-Moreno et al., 2005), planktonic foraminifers (Gonera et al., 2000; Bicchi et al., 2003), corals (Müller, 1984; Pisera, 1996), molluscs (Studencka et al., 1998; Harzhauser et al., 2003), and Crustacean decapods (Müller, 1984). Similar changes are also noticed for the Miocene of Central Europe in continental vertebrate faunas (Böhme, 2003) and in pollen assemblages (Jimenez-Moreno et al., 2005). This decline in temperature after the Middle Miocene Climatic Optimum (17 to 15 Ma) coincides with a worldwide cooling event generally attributed to the expansion of the Antarctic ice sheet (Zachos et al., 2001; Ohta et al., 2003; Westerhold et al., 2005).

The present study also shows the existence during the Badenian of a common stock of species, endemic Paratethyan and Mediterranean–Paratethyan, having little affinity with the Atlantic. The exchange of faunas between the Mediterranean and the Central Paratethys was probably regulated by an anti-estuarine circulation allowing normal marine surface water to enter the Mediterranean, while deeper hypersaline water flowed out from the Paratethys (Kókay, 1985; Báldi, 1997). This permitted an easier incursion of Mediterranean species into the Paratethys, but probably hindered the Paratethyan endemics from entering the Mediterranean. Another consequence was the concentration of salts towards the eastern part of the Central Paratethys, leading to the frequent deposition of evaporites in the Carpathian region (Kókay, 1985; Eastoe and Peryt, 1999; Peryt, 2001; Cendón et al., 2004). The same situation prevails in the present-day Gibraltar straits between the Atlantic and the Mediterranean. The deep-water Mediterranean current thus brings fewer bryozoan species into the Atlantic than the surface Atlantic current into the Mediterranean (Harmelin and d'Hondt, 1993). Although the deep hypersaline water flow coming from the Central Paratethys was an obstacle to the transfer of Paratethyan species to the Mediterranean, the origination of species within the Paratethys and their later transport into the Mediterranean cannot be ruled out.

Marine connections between the Indo-Pacific and the Mediterranean and Paratethys were interrupted during the late Early Miocene (Burdigalian). Even if intermittent seaways existed during the Middle and Late Miocene, faunal exchange of benthic marine invertebrates between the two bioprovinces was probably extremely limited.

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