

Palaeobiography of selected taxa of Miocene Bryozoa

KAMIL ZAGORŠEK

Department of Geography
Technical University of Liberec, Studentská 2. CZ-461 17 Liberec Czech Republic, e-mail: kamil.zagorsek@tul.cz

Abstract

Evidences for a bryozoan event during Badenian (Middle Miocene) time were recognized in several sections in north-south transect through the Paratethys. In each section the species composition was studied in detail. The majority of species involved in the bryozoan event are same in all studied sections. Nevertheless, a slight trend can be recognized. In the north sections bryozoans with erect growth forms are dominant, while in south sections prevail the species with encrusting and free living growth forms.

Easily recognizable bryozoan species *Pirabasporella*, *Skylonia*, *Costatimorpha* and representatives of family Chlidiopsidae were selected for palaeobiogeographic study. The distribution of these species from Eocene to Miocene (up to Recent respectively) show, that the Atlantic was not an obstacle for dispersal of bryozoans and the connection between the Paratethys and the Indian Ocean up to Australian waters can be explained through the shallow basins in Middle East. Moreover, the study suggests that the Paratethys was probably the biodiversity hot-spot during Eocene and Miocene; many genera later spread over the world originated here.

Keywords: palaeogeography, Bryozoa, Paratethys, Eocene, Miocene, palaeoecology

Introduction

Bryozoa represent an important part of the marine ecosystem. Their complicated morphology and taxonomy, however, often produces a rather low scientific interest; they are only rarely used for palaeoecological and palaeogeographical syntheses.

Within the last 20 years, this gap in knowledge has been partly filled, at least in the area of the Central Paratethys during the Miocene. When using bryozoans for palaeogeographical synthesis, the precise taxonomy is the most important basic information. Therefore, the detailed taxonomy and revision of the historical descriptions are essential needs for the forthcoming synthesis.

Beside the detailed complete taxonomy of Czech bryozoans (ZÁGORŠEK 2010), many areas around the world have been also studied by the author. Bryozoans from Austria (ZÁGORŠEK et al. 2011), Slovakia (ZÁGORŠEK 2007), Poland (ZÁGORŠEK et al. 2012), Turkey (ZÁGORŠEK & GORDON 2013), Germany (ZÁGORŠEK & GORDON 2014), Spain (ZÁGORŠEK et al. 2015), Romania (ZÁGORŠEK et al. 2010) as well as from Japan (ZÁGORŠEK et al. 2014), Brazil and Dominica (ZÁGORŠEK et al. 2014) have been studied. Excellent papers have been published dealing with Indo-

nesia (DI MARTINO & TAYLOR 2014), New Zealand (e.g. GORDON, STUART & COLLEN 1994) and unpublished results are known from Iran, Bulgaria, Libya and the USA.

After the taxonomic studies, the palaeoecology of Bryozoa became the author's main topic for research. Good examples of the "discovery" of Bryozoa as palaeoecological indicators are the so-called "bryozoan events" (ZÁGORŠEK 2010 or ZÁGORŠEK & KÁZMÉR 1999), which are usually easily recognizable in the sedimentological record. These events can be connected with specific palaeoenvironmental conditions, but, unfortunately, they have not been clearly explained. Interpretation of these conditions can give significant palaeoecological, palaeoceanographical and palaeogeographical data as well as information about the evolution of fossil ecosystems. This makes bryozoans an important group of invertebrates for palaeoenvironmental reconstructions.

Bryozoan event

Bryozoan accumulations are often elements of Cenozoic carbonate successions. Carbonate rocks in Eocene, Oligocene and Miocene sequences have been formed by coralli-

nacean algae, larger foraminifera and hermatypic corals (Eocene: Eastern Alps: RASSER 1994, 2000; Southern Alps: LUCIANI 1989, BASSI 1998; Slovenia: DROBNE et al. 1985, West Carpathians: SAMUEL et al. 1972; Oligocene: Southern Alps: FROST 1981; Slovenia: NEBELSICK et al. 2000; Miocene: Eastern Alps: DULLO 1983, FRIEBE 1990). At distinct levels they are interrupted by bryozoan accumulations (in the Eocene: West Carpathians: Gross et al., 1980, Zágorsk, 1992, 1994; Transdanubian Central Range: KÁZMÉR 1985, FODOR et al. 1992; Southern Alps: BRAGA in ANTOLINI et al. 1980; BRAGA & BARBIN 1988); Transyl-

The second factor may represent changes of trophic condition. Algae are adapted to oligotrophic conditions, whereas bryozoans prefer mesotrophic or eutrophic conditions. Increased organic production alone can suppress carbonate production of corals, larger foraminifers and calcareous algae (HALLOCK & SCHLAGER 1986, SENN & GLASSTETTER 1989), facilitating bryozoan accumulation.

As indicated by HOLCOVÁ & ZÁGORŠEK (2008), the main factor for bryozoan accumulation is probably changes in trophic condition, together with high variability of temperature (Figure 1).

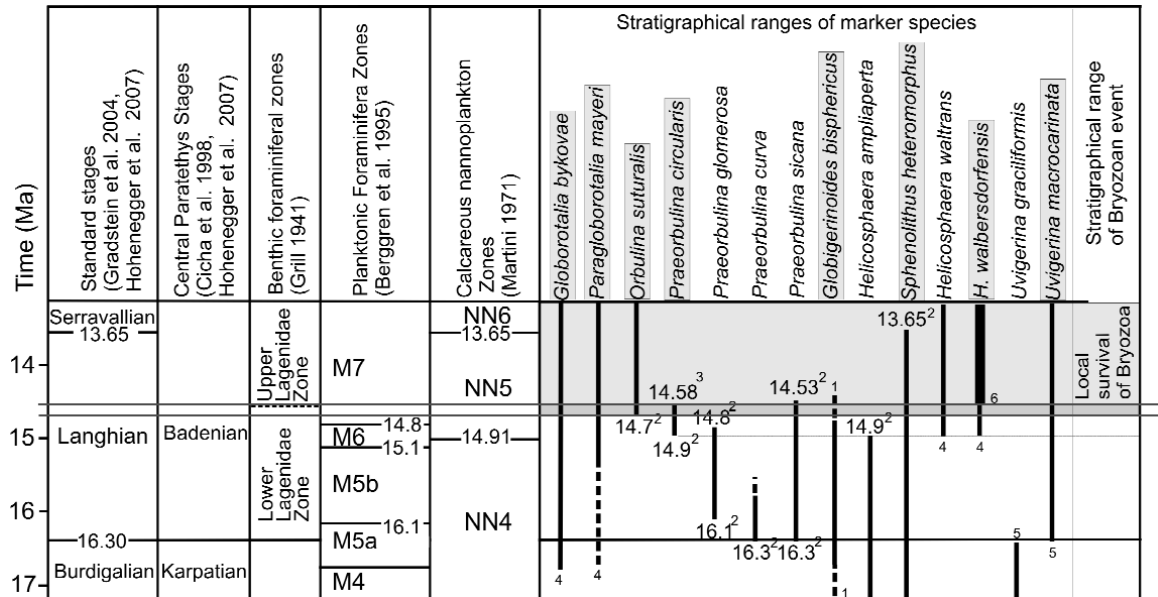


Figure 1. One of the time interval of studied bryozoan associations (from HOLCOVÁ & ZÁGORŠEK 2008)

vanian Basin: POPESCU et al. 1978; Oligocene: Southern Alps: UNGARO 1972; Miocene: Paratethys: VÁVRA 1979a, b, SAINT MARTIN et al. 2000).

Two palaeoenvironmental changes may explain changes from coral and algal accumulation to those of bryozoans. Common thought considers such bryozoan accumulations as indicators of short-time climate changes. Although climate oscillations of variable duration are well-known from the geological record, contemporaneous mangrove sedimentation (BÁLDI-BEKE 1984), among others, are counter-indicators of a cool climate.

Hermatypic corals prefer not to grow in seas where winter temperatures do not exceed 18 degrees (e.g. CHEN, 1999). Therefore, in mid- and high latitudes a major competitor to bryozoans is disqualified. Corallinean algae, another major competitor, like cool and even cold water, and can survive in the polar night (HENRICH et al. 1995). Since large accumulations of algae (algal rhodoliths) can live down to significant depths, both in tropical (IRYU 1992), temperate (WEHRMANN et al. 1995), and polar (FREIWALD 1998) or polar-influenced cool-water environments (JAMES & CLARKE 1997), their relative abundance in any one place is influenced by food supply.

Besides basic knowledge as taxonomy of the bryozoans and their palaeoecology, the research was finally aimed to find palaeobiogeographical rules of distribution of bryozoan fragments. The recent studies of palaeobiogeographical distribution of bryozoans enlarge the area of study to nearly the whole world. The data from Brazil, Japan, Dominica and Iran add valuable information to the use of bryozoans in palaeobiogeographical as well as palaeoecological synthesis.

As seen in the published data, several clearly distinguished families and genera have specific distribution patterns in time and space, while others show almost cosmopolitan spreading through the world's marine environments within the whole Neogene. The palaeobiogeographical value of bryozoan families with cosmopolitan distribution is very limited; only those with very detailed taxonomy may be useful. On the other hand, the families and genera with specific distribution patterns have high potential for palaeobiogeographical synthesis, and they might show new seaways connections and/or evolutionary pathways.

Miocene sediments in the Central Paratethys are rich in bryozoan fragments. The most diverse bryozoan associations were found during the Badenian (Figure 1).

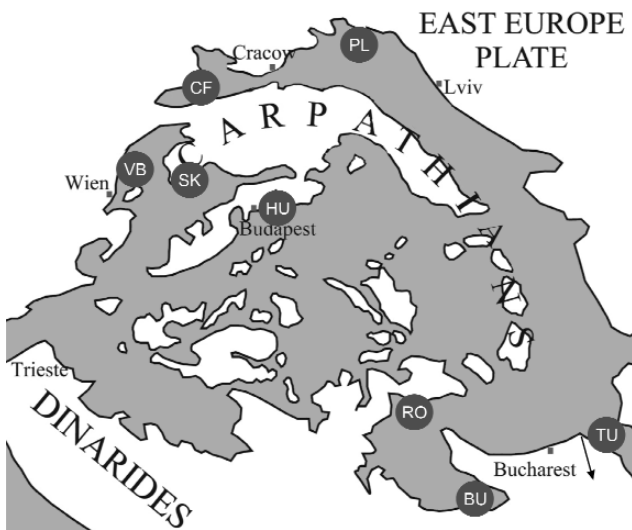


Figure 2. Position of the studied localities

Explanation of abbreviation: PL – sections in Poland, CF – Moravian part of Carpathians Foredeep, VB – Vienna basin, SK – sections in Slovakia, HU – sections in Hungary, RO – sections in Romania, BU – sections in Bulgaria, TU – additional section from Turkey (not in map, more in the south). Map based on GONCHAROVA et al. (2004) and BUKOWSKI et al. (2007), modified

Altogether eight different areas, more or less in a north south transect through the central Paratethys, were studied (Figure 2). The northernmost area belongs to the Carpathian foredeep in southern Poland (ZÁGORŠEK et al. 2012). More south are the Moravian part of the Carpathian foredeep and the Moravian part of the Vienna basin (ZÁGORŠEK 2010). The distribution of bryozoans in the Vienna basin was studied in detail mainly by VÁVRA (1979a), and additional research was completed recently (ZÁGORŠEK & VÁVRA 2007). Miocene bryozoans are quite rare in Slovakia compared to the other areas. Only a few localities yielded bryozoan fragments (ZÁGORŠEK & HUDÁČKOVÁ 2000, HOLCOVÁ et al. 1996). The data from the Hungarian localities were taken from MOISSETTE (2006). Miocene sediments in Romania yielded a very rich assemblage of Bryozoa (ZÁGORŠEK et al. 2010); this study is only partly finished, so for the synthesis unpublished data was used. The same applies also for the Bulgarian Miocene localities, where only a few bryozoan fragments were found. As additional data for comparison, Miocene sediments from central Turkey were taken into the consideration (ZÁGORŠEK & GORDON 2013).

Two hypotheses have to be tested. The first is that there will be a significant change from north to south in species composition, mainly reflecting the increase of temperature in the Central Paratethys. The second is that bryozoans from Mediterranean Turkey will differ from localities in Paratethys because of their much more southern position (more tropical environment with higher annual temperatures) and also because their palaeogeographical position in the basin is more open to the ocean, without connection to the somewhat restricted Paratethys.

Based on study of all sections, an idealized profile can be reconstructed (Figure 3). As visible from the picture, the basement of the profile consists of limestone to marl without bryozoans; it mainly contains foraminifers and echino-

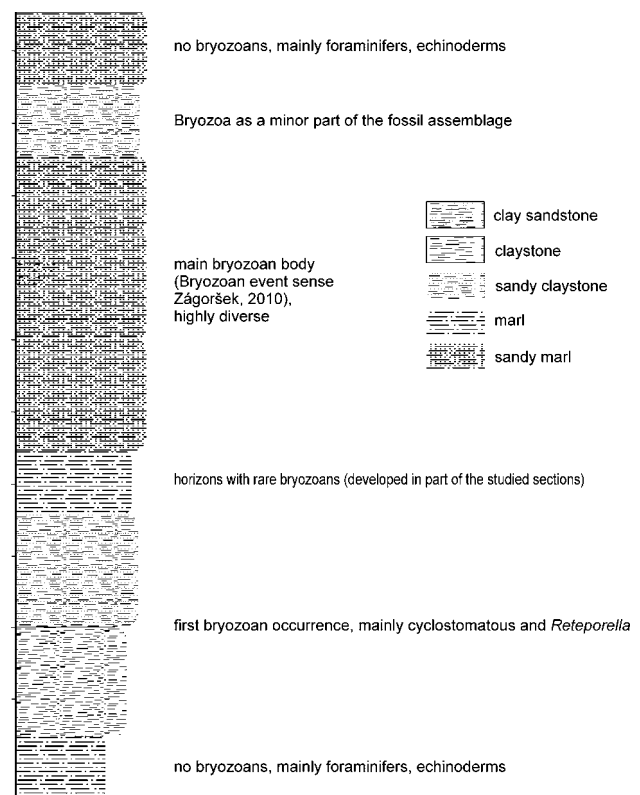


Figure 3. Idealized profile through the bryozoan-bearing sediments in Central Paratethys. The profile is valid not only for Miocene, but also in other time intervals during Neogene

derms. The first association of bryozoans occurred usually in marls and consists mainly of cyclostomatous genera and reteporids. Then follows the main bryozoan body with a highly diversified assemblage, often consisting of more than 150 species. This event of a massive occurrence of bryozoans and almost missing any other macrofaunal elements was named a Bryozoan Event (sensu ZÁGORŠEK 2010).

These two horizons were often interrupted by limestone with few bryozoans. The uppermost layers usually contain algae and/or molluscs; bryozoans are only the minor part of the fossil assemblage.

Twenty-five sections were studied in Poland. The sections Roztocze–Lisakow, Godziszow, Wendlinek; Holy Cross Mts — Korytnica and Zagrody yielded the most abundant associations of Bryozoa. In total, 75 species were determined. Characteristic members of the association are *Schizoporella? geminipora*, *Hagiosynodos latus*, *Tervia irregularis*, *Fron dipora*, *Onychocella*, *Lunulites*, *Cupuladria* and *Umbonula*. According to the ecological needs of the most abundant elements of the bryozoan fauna, the suggested environment was cool and deeper water, probably more than 100 to 150 m (presence of *Tervia* and *Fron dipora*) with algal meadows (due to the presence of *Schizoporella? geminipora*).

The presence of algal meadows is in contradiction with the presence of deep water species. Therefore, the final taphocenosis probably represent a mixture of several (or

only two?) original biotopes. The shallowest one is represented by algal meadows of depth not more than 50 m with *Schizoporella? geminipora*, and the deepest one is characterized by occurrence of *Tervia* and *Fron dipora*. The free living species (*Lunulites* and *Cupuladria*) may live in both suggested environment; their occurrence is limited by presence of hard surface and low water energy (ZÁGORŠEK et al. 2012).

The Moravian part of the Carpathians Foredeep is very rich in bryozoan fragments. Altogether 35 sections were studied; the most important for reconstructions are sections Podbřežice, Přemyslovice, Holubice, Kroužek, Oslavany, Rousínov and Práče. The total number of identified species is 156. The association is characterized by the presence of *Adeonellopsis*, *Onychocella*, *Hornera* cf. *frondiculata*, *Pleuronea pertusa*, *Reteporella*, *Puellina*, and *Exidmonea*. The original environment might be characterized by more humid and more dry periods in quite warm water conditions (water temperature from bryozoan skeleton 16.5–19.6 °C for *Reteporella*, 16.7–18.6 °C for *Smittina* and 18.2–22.1 °C for *Cellaria* (NEHYBA et al. 2008 and KEY et al. 2013) and very shallow, less than 20 m.

Miocene sections in Slovakia do not yield many bryozoan assemblages. Beside south Slovakia (HOLCOVÁ et al. 1996) and boreholes (ZÁGORŠEK & HUDÁČKOVÁ 2000), only two more sections (Sandberg and Devín-Merice) yielded bryozoans. Altogether 41 species were determined. The characteristic elements of the associations are *Myriapora*, *Hornera* cf. *frondiculata*, *Pleuronea pertusa*, *Umbonula*, *Margaretta*, *Tubulipora*, and *Crisidmonea*. Due to the presence of *Myriapora*, warm and shallow water was suggested, and because of presence of *Margaretta*, *Tubulipora* and *Crisidmonea*, high energy of water with strong wave activity and/or current might be expected in this area during Badenian.

The Miocene of Vienna basin and Molasse Zone in Austria are one of the most classical localities bearing bryozoan fragments studied already from the time of REUSS (1847). The most abundant sections are Rauchstall-brunngraben, Brugg and Eisenstadt with total determined species of 147 (VÁVRA 1979a and personal communication, 2015). Characteristic members of this association are *Schizoporella*, *Steginoporella*, *Umbonula*, *Margaretta*, *Eschara* and *Pleuronea*. According to the palaeoenvironmental reconstruction, the original conditions in the Badenian were warm and shallow water with sandy beaches containing abundant brachiopods *Terebratula* (WESSELY 2006, ZÁGORŠEK & VÁVRA 2007).

The sections Szentkút and Kemence in Hungary yielded the most abundant and diverse bryozoan assemblage from all studied sections. Altogether, more than 180 species were determined (MOISSETTE et al. 2006 and own unpublished study). Characteristic members of this association are *Margaretta cereoides*, *Adeonella polystomella*, *Smittina cervicornis*, *Steginoporella*, *Crisia*, and *Escharoides*. MOISSETTE et al (2006) suggested very warm and shallow water, upwards deepening, quiet environment with low water

energy.

Sections Gîrbova de Sus, Lapugiu, and Moldovenești were studied in detail in Romania. They yielded altogether 92 bryozoan species with characteristic members of association *Vibracella trapezoida*, *Poricella*, *Steginoporella* and *Adeonella polystomella*. Due to the presence of these faunal elements, warm and deep water (more than 50 m) probably influenced by underwater currents, with intervals of shallowing might be suggested (ZÁGORŠEK et al. 2010).

Only unpublished data are available from Bulgaria, where only the Yasen section yielded bryozoan fragments. Preliminarily, 15 species were determined, characterized by *Amphiblestrum appendiculatum*, *Retepora* sp., *Pleuronea pertusa*, *Cribelopora*, *Reussirella*, and *Hippoporina*. Warm, low-energy sea and stable bottom is expected in this area mainly due to the presence of *Cribelopora*, *Reussirella* and *Hippoporina*.

For comparison, a section outside the Central Paratethys was chosen to show the principal differences in bryozoan composition. Section Başıyayla is situated in the central Anatolian Plateau in southern Turkey. Altogether 36 bryozoan taxa were identified; among them dominate *Cupuladria*, *Reussiella haidingeri*, *Hippoporella*, *Nellia* cf. *oculata* and two new genera: *Basyaylella* and *Ostrovskia*. Warm, subtropical water and depth up to 100m, with hard substratum and low energy is suggested (ZÁGORŠEK & GORDON 2013)

As visible on Figure 4, the composition of the bryozoan assemblages in the studied sections changed. Some trends might be observed. In the northern part, the most dominant are erect rigid forms, mainly from cyclostomatous order and genera like *Smittina*, *Adeonella*, *Onychocella*. Going more south, more encrusting and erect flexible forms dominate, like *Vibracella* and *Umbonula*. In the southernmost part the free-living genera like *Reussirella*, *Cupuladria* and/or



Figure 4. Characteristic faunal elements of studied area with visible trends of domination of free-living and encrusting colonies in direction to south. Only in Turkey, the dominant species was flexible erect
Explanation of abbreviation: En = encrusting, Er = erect, Fl = free living (map based on GONCHAROVA et al. 2004 and BUKOWSKI et al. 2007, modified)

Lunulites form a considerably larger portion of bryozoan assemblage than in northern sections. The bryozoan association in Turkey is quite different from the Central Paratethyan ones. It differs mainly in presence of *Nellia* cf. *oculata* and two new genera *Basayayella* and *Ostrovskia*, which belong to families having no representatives in the Central Paratethys.

However, these changes are not significant. Almost the same species dominate in all sections; only the Bryozoa associations from Turkey are different. It contains families that are not present in any other sections, and also the suggested environment is different, tropical condition in deep water is expected. Some general trend might be observed: the dominance of tropical elements is slightly increased from north to south (from *Tervia*, *Metrarabdotos*, *Onychocella*, *Schizoporella geminipora* to *Cribelopora*, *Nellia*, *Reussirella* and *Steginoporella*).

We can therefore assume that local environmental conditions blurred the latitudinal differences.

These results might be, however, caused also by other factors, not only by the original composition of the bryozoan assemblages. Complete and precise taxonomical study is still not finished in many sections; plenty of minor and less abundant species have not been identified yet. Moreover, the studied material is not fully comparable; from Moravia and Poland were studied more than 20 sections, while from Rumania only 3 sections, and from Bulgaria and Turkey only one section was studied. According to these results, a new question is raised: do only minor differences in species composition mean that the palaeoenvironmental conditions in Paratethys were uniform? Is it possible, that there were no significant change in temperature, food supply, salinity from north to south on a scale of about 800–1000 km? Hopefully, the answer will be given in forthcoming years.

Palaeobiogeography of selected taxa

For palaeobiogeographical synthesis the most suitable taxa are easily identifiable and therefore the mistake in interpretations caused by comparison of different taxa are minimised. For the synthesis also historical data can be used, without detailed and precise taxonomy. Taxa with complicated and very similar morphology (like most common families Smittinidae or Hippoporididae) are often misinterpreted in historical papers due to the lack of sophisticated techniques, especially scanning electron microscopy at that time. In the meantime taxa with specific morphological features might be often correctly identified in historical publications, or can be easily revised and reinterpreted even from drawings. For the palaeobiogeographical reconstruction based on bryozoan fragments we chose families with very distinct features like Jaculinidae ZABALA, 1986 (Figure 5), Skyloniidae SANDBERG, 1963 (Figure 6), Chlidiopsidae HARMER, 1957 (Figure 7) and

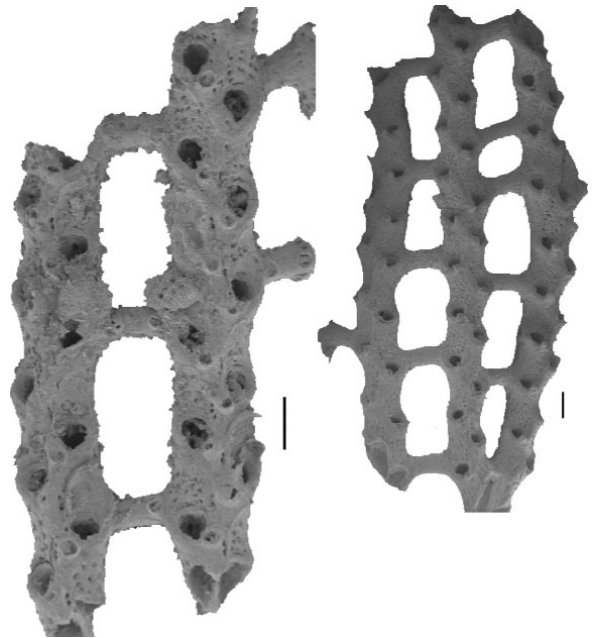


Figure 5. Genus *Pirabasporella* ZAGORSEK et al. 2014 as representatives of family Jaculinidae ZABALA, 1986 from Pirabas formation, Brazil. Scale bars 100 μ m

genus *Costaticella* MAPLESTONE, 1899 from the family Catenicellidae BUSK, 1852 (Figure 8).

All these taxa are easy to determine and hard to

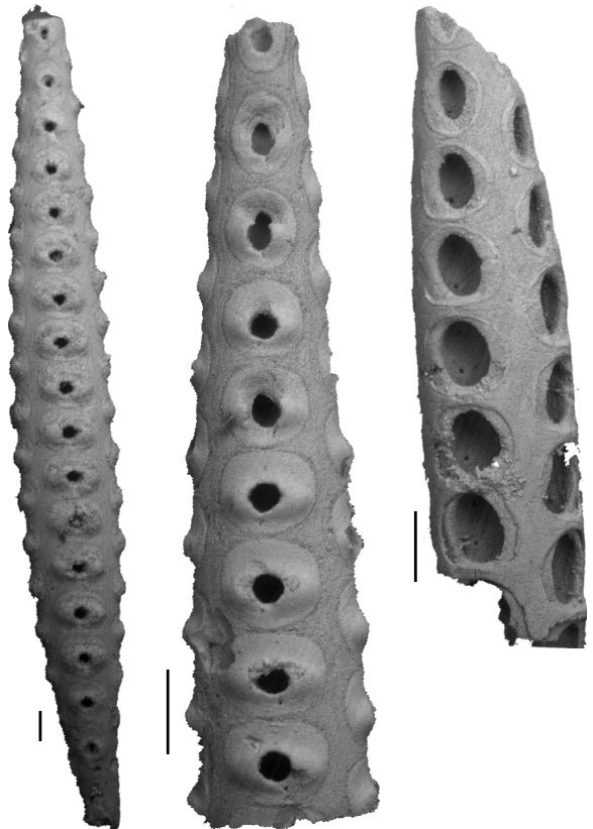


Figure 6. *Skylonia dohmi* as representatives of family Skyloniidae SANDBERG, 1963 from Pirabas formation, Brazil. Scale bars 100 μ m

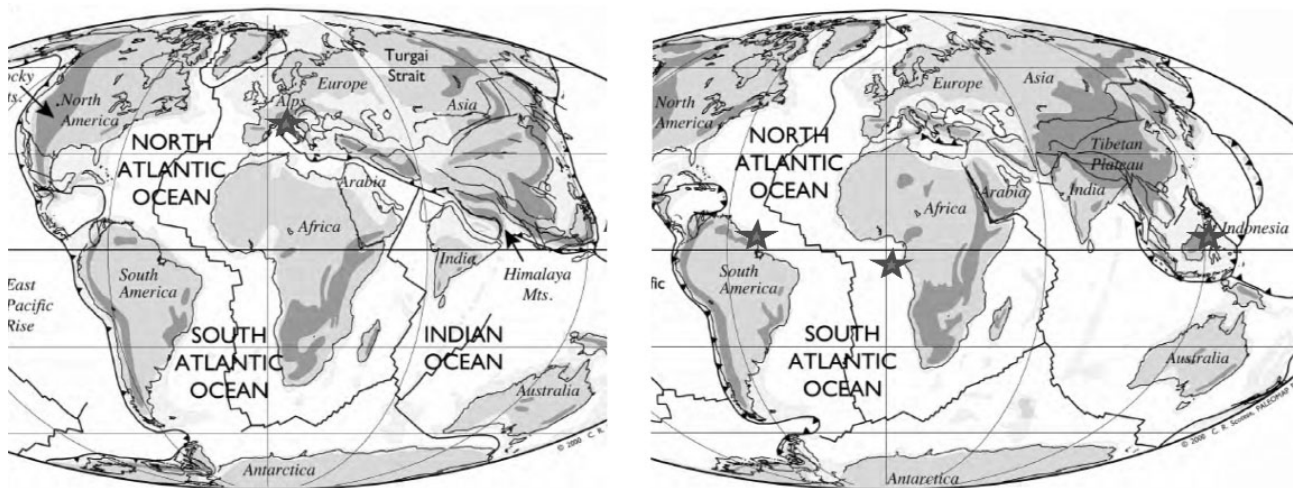


Figure 7. Distribution of family Skylloniidae SANDBERG, 1963 in time and space from Eocene (left) to Miocene (right). Palaeogeographic maps from SCOTSE (2001)

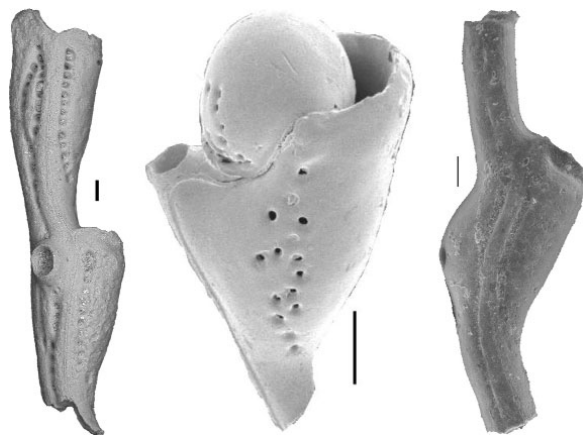


Figure 8. Representatives of Chlidiopiidae (from left to right): *Celiopsis vici*, *Chlidiopsis inopina* and *Celiopsis vindobonensis*. Scale bars 100 μ m

misinterpret. Jaculinidae is characterized by dissepiments between branches bearing autozoecia, a feature not present in any other family (ZÁGORŠEK et al. 2014). Skylloniidae is characterized by unique morphology and shape of colonies, which cannot be found in any other bryozoan group. The presence of unizooecial, flexible erect colonies with long stolons characterizes family Chlidiopiidae (ZÁGORŠEK et al. 2015). The genus *Costaticella* MAPLESTONE, 1899 from family Catenicellidae BUSK, 1852 is characterized by two distinct oral avicularia and costal part of the frontal shield, which cannot be misinterpreted with any other known bryozoan genus.

Besides published data about these taxa, much unpublished information was made available thanks to my own study and to personal communication with colleagues, especially from Brazil (Laís RAMALHO from Rio Grande de Sus University) and Australia (Phil BOCK from Technical University Mount Waverley) and Emanuela DI MARTINO, who studied Indonesian Miocene bryozoans. Also my own unfinished studies from sections Europe, Iran and Libya are part of the reconstruction.

The oldest representative of the family Jaculinidae ZABALA, 1986, genus *Pirabasoporella* occurs in Brazil and

Dominica (ZÁGORŠEK et al. 2014): it is Miocene. In Recent Jaculinidae, which occur at ~200–1250 m depth (*J. blanchardi* 230–980 m; *J. dichotoma* 1250 m; *J. tessellata* 460–1000 m), in the eastern Atlantic and Mediterranean (own observation and personal communication of Bjorn BERNING).

The main difference between fossil western Atlantic *Pirabasoporella* and eastern Atlantic and Mediterranean Jaculinidae is the perforate frontal shield in the former. Recent species have only a single row of lateral areolar pores, whereas in *Pirabasoporella* at least the proximo-median part of the frontal shield is perforated and the latero-abfrontal areas contain more pores. Porous and imperforate frontal shields are not unusual in sister genera, while, according to GORDON (2000), the porous frontal shield is considered to be the derived character.

Early Miocene *Pirabasoporella* with its perforate frontal shield clearly predates the Pleistocene to Recent eastern Atlantic/Mediterranean clade, and may counter this hypothesis. However, most Jaculinidae seem to occur at bathyal depths (but see below), the sediments of which have only a sparse fossil record. It is thus likely that the present temporal sequence of occurrence is a sampling artefact. Moreover, the presence of jaculinid clades on both sides of the Atlantic argues for a considerable history of the group. Their adaptation to soft sediments, and their reproduction via short-lived trochophore larvae, makes it unlikely that species have crossed the ocean by rafting on floating objects or via their larval stage, respectively. Dispersal via abyssal basins seems equally unlikely given the precipitation of calcitic skeletons in jaculinids. The most probable scenario is an early Palaeogene origin of the Jaculinidae when the continental shelves of the Atlantic were positioned considerably closer together. All fossil and Recent jaculinid species have been found in tropical to warm-temperate regions, while there are no records of Recent Jaculinidae from the western Atlantic to date.

Skylloniidae SANDBERG, 1963 first occurs in the Eocene of Austria (ZÁGORŠEK 2003) and later occurs during the Miocene in many areas (Brazil, Dominica, tropical Africa

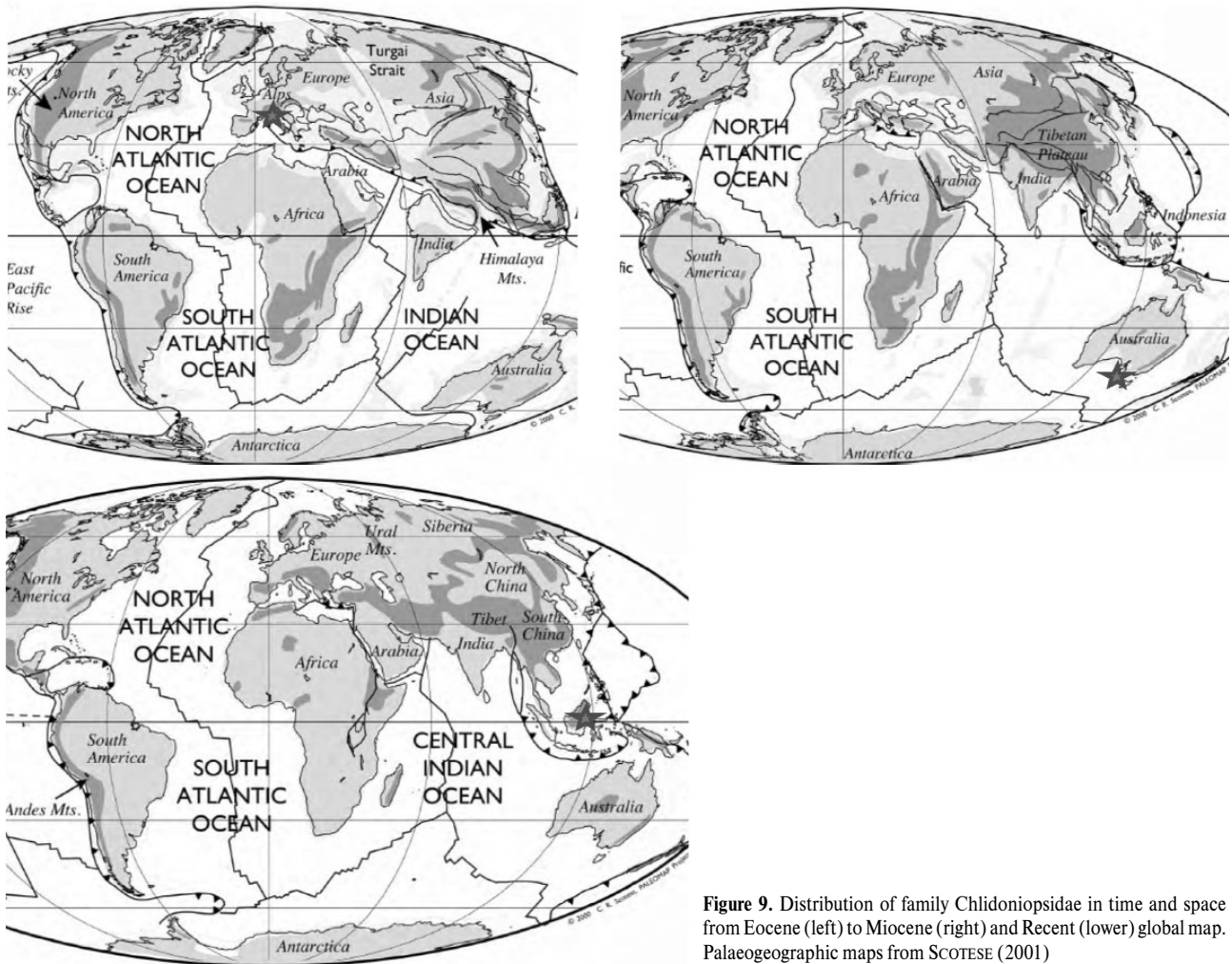


Figure 9. Distribution of family Chlidoniopsidae in time and space from Eocene (left) to Miocene (right) and Recent (lower) global map. Palaeogeographic maps from SCOTSE (2001)

and Indonesia (ZÁGORŠEK personal observation; DI MARTINO & TAYLOR 2014). No recent skylonids are known.

As visible from Figure 7, the skylonids from the Eocene to Miocene spread in south in almost all directions. While the presence of skylonids in South America can hardly be explained by direct transport through the Atlantic Ocean (similar to the jaculinids), the dispersal via open shallow basins between Africa and Middle Asia to Kalimantan might be easily explained.

Another good example of bryozoan dispersal from Eocene to Miocene might be shown also by the family Chlidoniopsidae (Figure 8).

The two genera of Chlidoniopsidae are clearly separated not only morphologically, but also geographically and chronostratigraphically (Figure 9). The two species of *Chlidoniopsis* occur from the Miocene of Victoria, Australia, to the Recent of equatorial Indonesia (just south of the equator). The three species of *Celiopsis* occur in the Northern Hemisphere only from the Buda Marls, Hungary (ZÁGORŠEK 2001), the Waschberg Zone, Austria (ZÁGORŠEK 2003), the Molasse zone (Vicentin, Italy) and the Eastern Alps, Poland, Slovakia and the Vic basin (Spain) (ZÁGORŠEK 2003). The temporal range of the genus is from the late Eocene of Hungary (ZÁGORŠEK 2001), late Eocene

(Priabonian) of Catalonia, Austria, Poland, Slovakia, Hungary and northern Italy, and the early Oligocene (Rupelian) of Lower Austria (see VÁVRA 1994; ZÁGORŠEK et al. 2012). Accordingly, the family appears to have originated in the Paratethys, migrating to eastern Tethys (Val di Lonte, Italy) as well as to western Tethys (*C. vici* from Vic of Spain) during the Late Eocene. Eocene *Celiopsis* is clearly already jointed. This evolutionary innovation was conserved in

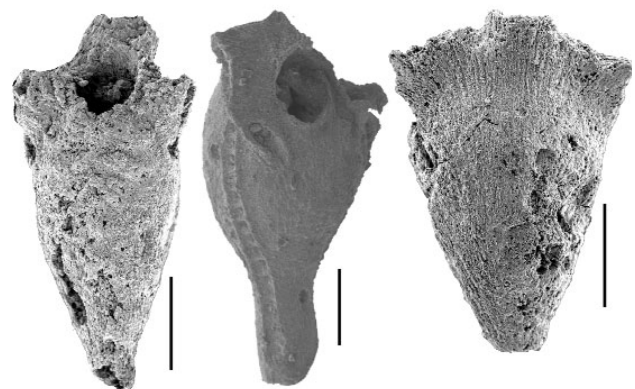


Figure 10. *Costatimorpha* ZÁGORŠEK, 2003 as Eocene representative of genera similar to *Costaticella* and Brazilian representative from Miocene of Pirabas formation. Scale bars 100 µm

Chlidoniopsis. Recent *C. inflate* from Indonesia is so similar to *C. inopina* from the Miocene of Australia, that a degree of evolutionary stasis in the Neogene can be assumed (ZAGORŠEK & GORDON 2015).

As a last example of spatial distribution of Bryozoa, the group of genera similar to *Costaticella* MAPLESTONE, 1899 might be used. It is also a very distinct genus (Figure 10) with presence of costal part of the frontal shield as the characteristic feature.

Costaticellids has similar dispersal pattern as the previous families (Figure 11). The oldest representative is known from the Eocene of Hungary (ZAGORŠEK 2003). During the Miocene the group was found in Brazil, and recently the genera *Costaticella* is known in waters around Australia (GORDON pers. comm. 2015).

It seems that the Atlantic is not an obstacle for the distribution of the bryozoans from the Eocene to Miocene (in both ways). Connection between the Paratethys and the Indian Ocean through the shallow basins in Middle East can explain the dispersal of Bryozoa into Australian waters.

Moreover, Paratethys was a biodiversity hot-spot; many genera originated here (not only these mentioned here, but several others additional genera have the oldest occurrence in Paratethys) like *Bactridium*, *Poricella*, *Caberoides* and

many others.

However, all these hypotheses may be significantly affected by overstudied European and Australian fields and understudied exotic fields (like Indonesia, Brazil and sections in Africa and Middle East). To support this hypothesis would be the work for forthcoming years.

Conclusions

Bryozoan Event can be identified in many sections in Paratethys during Badenian (middle Miocene). However the species involved in the Bryozoan event do not changed significantly from north to south. The distribution of the species shows slight trend from dominance of erect growth forms in north to dominance of encrusting and free living growth forms in south. But the majority of species are same. Does it mean that the palaeoenvironmental conditions in Paratethys were uniform? Is it possible, that there were no significant change in temperature, food supply, salinity from north to south on a scale of about 800–1000 km?

The distribution of selected, easily recognizable bryozoan species shows that the Paratethys was probably the

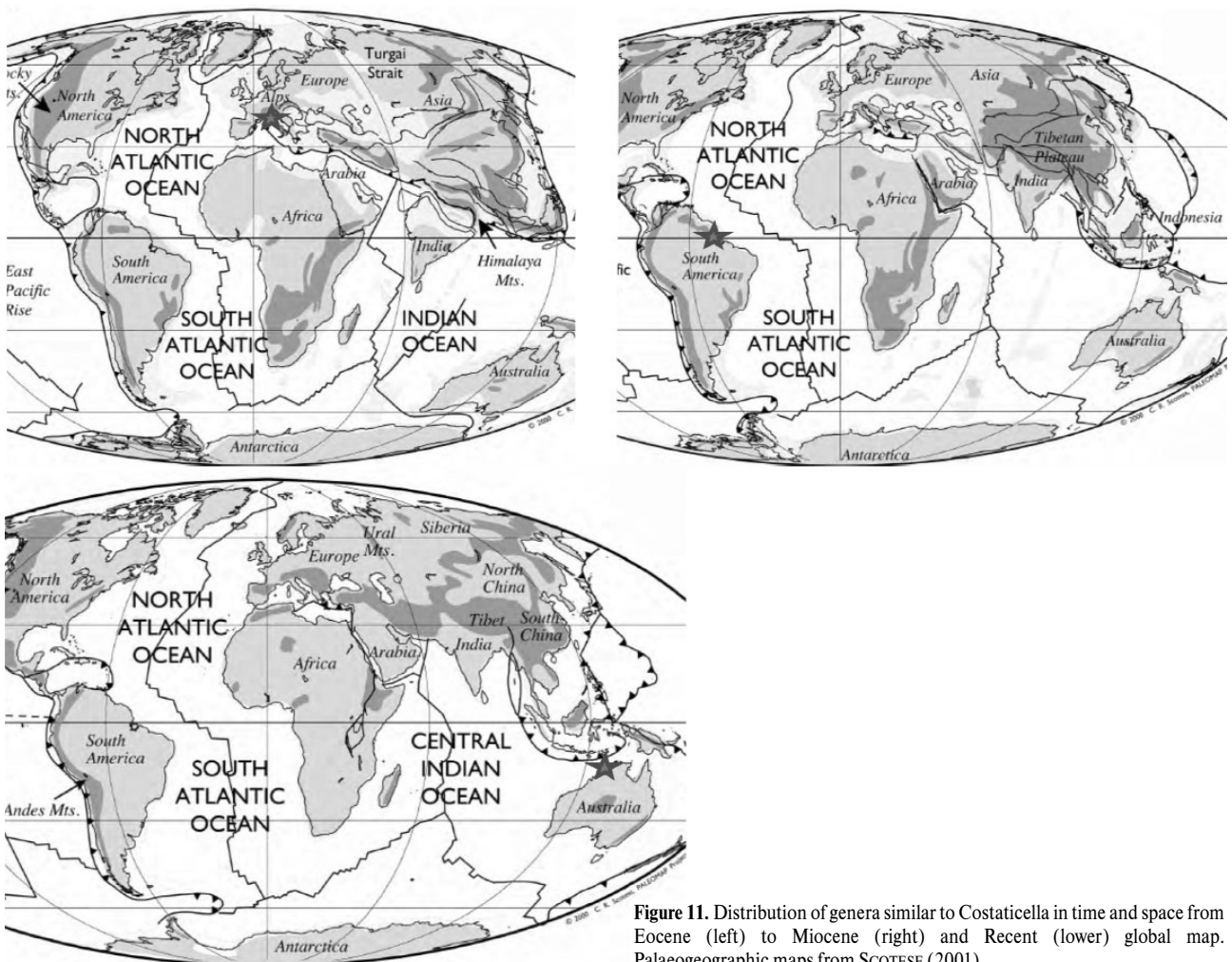


Figure 11. Distribution of genera similar to *Costaticella* in time and space from Eocene (left) to Miocene (right) and Recent (lower) global map. Palaeogeographic maps from SCOTSE (2001)

biodiversity hot-spot; many genera later spread over the world originated here (skylonids, chlidoniopsids, costatelids and many others). Moreover, the Atlantic was not an obstacle for the distribution of the bryozoans from the

Eocene to Miocene (in both ways) to America. Connection between the Paratethys and the Indian Ocean up to Australian waters can be explained through the shallow basins in Middle East.

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