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ORIGINAL PAPER

Paleoenvironmental reconstruction of the Early to Middle Miocene Central Paratethys using stable isotopes from bryozoan skeletons

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Abstract Stable carbon and oxygen isotope values from single bryozoan colonies were used to reconstruct the paleoenvironments of the Early to Middle Miocene (Ottnangian to Badenian) sediments of the Central Paratethys. This approach utilizes a locally abundant allochem while avoiding matrix and multiple allochem contamination from bulk rock samples. Bryozoan colonies (and a few foraminifera and rock matrix samples) from 14 localities yielded 399 carbon and oxygen isotope values. Data from six of the localities (15 % of the total number of samples) were interpreted as having been diagenetically altered and were rejected. The remaining data indicate a primarily localized upwelling signal with lesser variation caused by global climatic and regional tectonic forcing of sea level, salinity, and temperature. Paleotemperatures were calculated to range from 12 to 21 °C. Despite potential taxonomic and diagenetic problems, bryozoan colonies are a powerful, underutilized source of paleoenvironmental carbon and oxygen isotope data.

Keywords Miocene · Bryozoa · Stable isotopes · Central Paratethys

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Introduction

The use of $\delta^{13}C$ and $\delta^{18}O$ values for paleoenvironmental interpretation of the Central Paratethys in the Miocene has only been applied to a few select allochem types including foraminifera (Durakiewicz et al. 1997; Gonera et al. 2000; Báldi 2006; Kováčová et al. 2009), molluscs (Hladilová et al. 1998; Bojar et al. 2004; Latal et al. 2004, 2006), brachiopods (Bojar et al. 2004), and bryozoans (Holcová and Zágoršek 2008; Nehyba et al. 2008a). Bryozoans have a long history of utilization in paleoenvironmental reconstruction (Smith 1995). The traditional methods took an actualistic approach based on the known ecology of extant species (e.g., Moissette 2000; Moissette et al. 2007) or the analysis of colony growth form (e.g., Hageman et al. 1997). More quantitative methods have also been developed. The relative partitioning of intra- versus intercolony morphologic variation has been used as a proxy for water depth (e.g., Key 1987). More recently, zooid dimensions have been used as a proxy for mean annual range in temperature (e.g., O'Dea 2003). The most common method in bryozoans uses oxygen isotopes to calculate absolute paleotemperatures (e.g., Knowles et al. 2010).

Bryozoan skeletons are generally underutilized as sources of stable isotope information for paleoenvironmental reconstruction due to taxonomic difficulties and potential problems common with all biogenic carbonate sources. These potential problems include (1) diagenesis, (2) intracolony variation, and (3) vital effects (e.g., Crowley and Taylor 2000; Smith et al. 2004; Nehyba et al. 2008a).

When determining stable isotope values of fossil skeletons, diagenesis of bryozoans, as with any carbonate source, may obfuscate the original environmental record (see review in Key et al. 2005a). Carbonate diagenesis

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includes compaction, dissolution, neomorphism (i.e., recrystallization), as well as cementation, all variably significant in lithification of carbonate sediments. As discussed below, the samples in this study have not been lithified suggesting their diagenesis is potentially less than that in carbonate rocks.

The degree of intracolony variation in stable isotope values has not been sufficiently quantified, but see Smith et al. (2004) and Smith and Key (2004) for some preliminary results. In contrast, vital effects are more of a concern as they have only been indirectly ruled out in some fossils (e.g., Key et al. 2005b). Vital effects are also a problem in more commonly used sources of isotopes such as foraminifera and molluscs. For example, Gonera et al. (2000) had to deal with vital effects in *Globigerinoides* spp. as part of their study of isotope values from Badenian foraminifera in the Central Paratethys. Bojar et al. (2004) reported vital effects in the isotopes of molluscs from the early Badenian Styrian Basin, Austria. Latal et al. (2006) reported a vital effect in one of their molluscs in their study of the early Badenian of the Northern Alpine Foreland Basin.

The goal of this study is to use $\delta^{13}C$ and $\delta^{18}O$ values from single bryozoan colonies to reconstruct the paleoenvironments of the Early to Middle Miocene sediments of the Central Paratethys. Using single bryozoan colonies avoids the problems of bulk sampling, that is, the mixing of isotopic signals from various sources. For example, bulk sampling can mix rock matrix, different phases of cementation, and different allochems, each of which may have a different isotope value. Likewise, the different allochems may have different vital effects. In addition to these carbonate sources having different isotope values, they may also have a different volumetric proportion in a bulk sample (e.g., Kováčová et al. 2009). This kind of contamination by matrix was cited as a possible source of isotope variation between replicate samples in Gonera et al.'s (2000) study of isotope values from Badenian foraminifera in the Central Paratethys as well as in Nehyba et al.'s (2008a) study of isotope values from lower Badenian bryozoans in the Carpathian Foredeep of the Central Paratethys.

Early to Middle Miocene geologic setting

By the Miocene, the ancient Tethys Ocean had been replaced in its western part by two relict seas, the Mediterranean and the Paratethys (Rögl 1998, 1999; Cornée et al. 2009). From the end of the Eocene to the Middle Miocene, the Paratethys was an enclosed sea consisting of a series of basins that experienced repeated isolation episodes, with narrow, intermittent seaways connecting it not only to the Atlantic Ocean and Mediterranean Sea but also to the Indo-Pacific and even to the Boreal Ocean (Rögl 1998, 1999; Steininger and Wessely 2000; Meulenkamp and Sissingh 2003; Popov et al. 2004, 2006; Latal et al. 2006). During the Early to Middle Miocene, the Central Paratethys (i.e., the area from present-day Austria to Poland and Romania; Fig. 1a) underwent a variety of regional tectonic and global climatic changes. These external forcing mechanisms impacted the local paleogeographic geometries and oceanographic settings which affected water depth/sea level, water circulation, salinity, temperature, and upwelling, as well as the evolving marine biota (Rögl 1998; Kováč 2000; Popov et al. 2004; Harzhauser and Piller 2007). During most of the Early to Middle Miocene, thick marine sediments were deposited throughout the Central Paratethys (Vakarcs et al. 1998). These sediments included numerous bryozoans (Moissette et al. 2007).

Materials and methods

Bryozoan-rich, Early to Middle Miocene sediments from the Eastern Alpine Foredeep, Carpathian Foredeep, Vienna, Eisenstadt, and Nograd Basins of the Central Paratethys were sampled at 14 localities ranging in age from ~18 to 14 Ma (Table 1; Fig. 1b). The 12 younger localities (~16 to 14 Ma) came from calcareous nannofossil zones NN4 and NN5 (Table 1). Based on Hohenegger et al. (2009), this places them in the lower to middle Badenian (Fig. 2). The Badenian is a regional stage used in the Central Paratethys, and its lower part is equivalent to the Langhian stage of the Middle Miocene epoch (Piller et al. 2007) (Fig. 2). The Badenian stage in the Central Paratethys spans from 16.303 to 12.73 Ma (Hohenegger et al. 2009; Hohenegger and Wagreich 2012) (Fig. 2). The base of the Langhian, as dated by Gradstein et al. (2004), is 15.97 Ma. The top is dated at 13.82 Ma (Hilgen et al. 2009). The two older localities (~18 Ma) came from near the boundary between calcareous nannofossil zones NN3 and NN4 (Table 1). Based on Hohenegger et al. (2009), this places them in the Ottnangian (Fig. 2). Our samples span the Badenian "Bryoevent" of the Central Paratethys (Zágoršek 2010a). The 15–14 Ma bryoevent preserved in the Middle Miocene of the Central Paratethys represents a short period of time with a sudden and massive occurrence of a highly diverse bryozoan fauna (Zágoršek 2010a).

All of the localities but Přemyslovice, which came from a shallow core at 100 cm depth, were from surface exposures. Bulk samples were collected with stratigraphic control and with a preference for bryozoans. The bulk samples were split into three roughly equal-sized subsamples: (1) non-skeletal archival sample, (2) non-skeletal rock

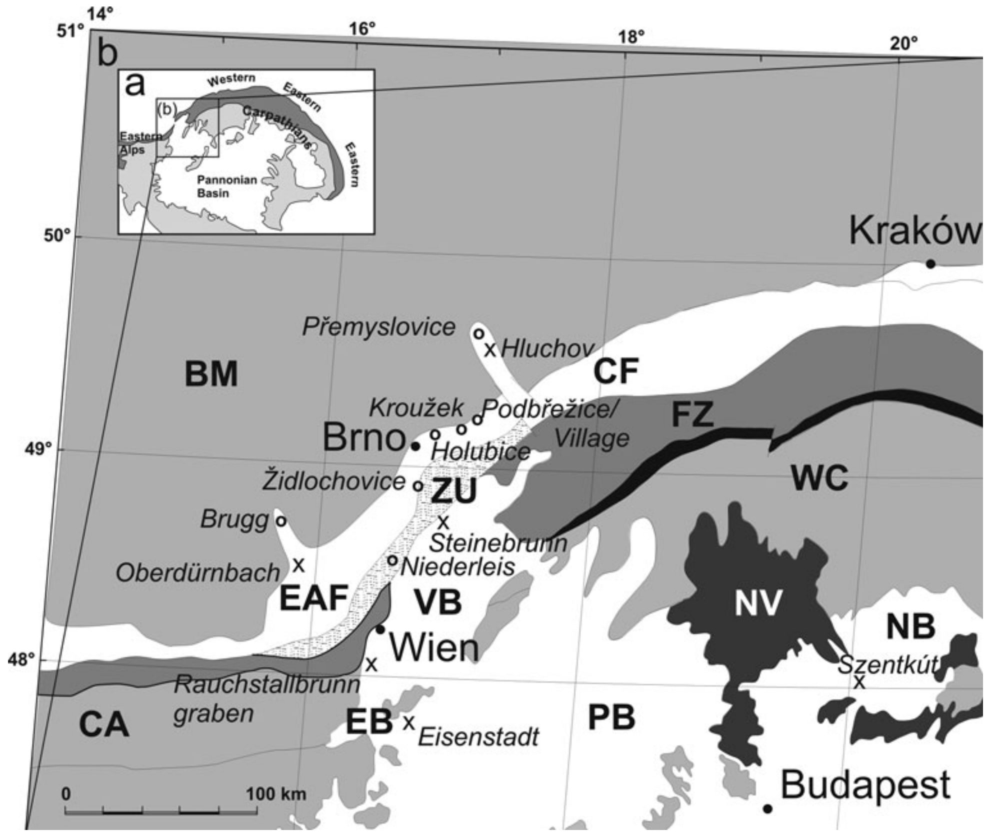

Fig. 1 **a** Paleogeographic map of the Central Paratethys during the Early to Middle Miocene. **b** Sampling localities in italics relative to major regional European cities and the Eastern Alpine Foredeep (*EAF*), Ždánice Unit (*ZU*), Carpathian Foredeep (*CF*), Vienna Basin (*VB*), Eisenstadt Basin (*EB*), Pannonian Basin (*PB*), Nograd Basin (*NB*), Bohemian massif (*BM*), Calcareous Alps (*CA*), Flysch Zone (*FZ*), Western Carpathians (*WC*), and Neovolcanics (*NV*). *o* indicates locality included in final analysis, whereas *x* indicates locality excluded from final analysis due to diagenetic alteration

matrix sample, and (3) skeletal sample to be washed for bryozoans. None of the samples were lithified by cementation to require sectioning. The samples from Podbřežice had higher clay content and were slightly cemented so they did not readily disaggregate during wet sieving. Before being wet sieved like all the other samples, those from Podbřežice were boiled in water for ~10 min, then frozen for 4 h at −18 °C then melted and wet sieved. The samples were wet sieved through stacked 0.9- and 1.0-mm sieves. The samples were ultrasonically cleaned for ~2 min. The samples were then washed again with water and placed in an 85 °C oven for drying. The 0.9- and 1.0-mm fractions were picked under a binocular reflected light microscope for foraminifera and bryozoans, respectively. Most of the bryozoans were identified to the genus level. The non-*Amphistegina* foraminifera were set aside for later biostratigraphic analysis.

The foraminifera and bryozoans from the slightly cemented locality (Podbřežice) were examined using cathodoluminescence and found to have only one generation of calcite cement (Nehyba et al. 2008a). The most pristine bryozoans and *Amphistegina* foraminifera were selected based on the lack of any diagenetic infilling cements, lack of evidence of recrystallization, and lack of encrusting organisms. These were then reprocessed through the ultrasonic cleaner, and re-dried. At least one colony per bryozoan genus per locality as well as two non-skeletal rock matrix samples per locality were selected. These were then separately ground into powder with a non-carbonate mortar and pestle.

The samples were roasted in a vacuum at 200 °C for 1 h to remove water and volatile organic contaminants that may confound stable isotope values of carbonates. Stable isotope values were obtained using a Finnigan Kiel-IV carbonate preparation device directly coupled to a Finnigan MAT 253 isotope ratio mass spectrometer. From 20 to 50 µg of carbonate was reacted at 70 °C with 3 drops of anhydrous phosphoric acid for 420 s. The CO_2 evolved was then cryogenically purified before being transferred to the mass spectrometer for analysis. Isotope ratios were corrected for acid fractionation and ^{17}O contribution using the Craig (1957) correction and reported in per mil notation relative to the VPDB scale. Data were directly calibrated against the international standard NBS-19 that is by definition $\delta^{13}C = 1.95$ ‰ VPDB and $\delta^{18}O = -2.2$ ‰ VPDB. Accuracy of data was monitored through routine analysis of NBS-19 and in-house check standards which have been stringently calibrated against NBS-19. Accuracy of $\delta^{13}C$ and $\delta^{18}O$ were 0.05 and 0.11 ‰, respectively.

Table 1 Locality information arranged by age

Locality name, country	Depositional basin	Age (~Ma)	Support for age	Source of detailed locality and age information
Rauchstallbrunngraben, Austria*	Vienna	14	Foraminifera biostratigraphy indicates Upper Lagenid Zone in calcareous nannofossil zone NN5 in the lower Badenian	Kroh (2005); personal observation of M. Harzhauser
Eisenstadt, Austria*	Eisenstadt	14.5	Foraminifera biostratigraphy indicates the uppermost Lower Lagenid Zone to the boundary with the Upper Lagenid Zone in calcareous nannofossil zone NN5 in the lower Badenian	Kroh et al. (2003)
Niederleis, Austria	Vienna-Eastern Alpine Foredeep transition	14.5	Foraminifera and mollusc biostratigraphy indicates upper part of Lower Lagenid Zone in calcareous nannofossil zone NN5 in lower Badenian	Cicha et al. (1998); Mandic et al. (2002)
Podbřežice village, Czech Republic	Carpathian Foredeep	14.5	Presence of the foraminifera *Orbulina suturalis* whose FAD indicates < 14.56 Ma at the top of the Lower Lagenid Zone in calcareous nannofossil zone NN5 in the uppermost part of the lower Badenian	Zágoršek and Holcová (2005); Di Stefano et al. (2008)
Steinebrunn, Austria*	Vienna	14.5	Foraminifera and mollusc biostratigraphy indicates upper part of Lower Lagenid Zone in calcareous nannofossil zone NN5 in lower Badenian	Grill (1968); Zágoršek and Vávra (2007); Paulissen et al. (2011)
Židlochovice, Czech Republic	Carpathian Foredeep	15	Foraminifera biostratigraphy indicates calcareous nannofossil zone NN5 in the lower Badenian	Cicha (1978); Zágoršek (2010b)
Holubice, Czech Republic	Carpathian Foredeep	15	Approximated from personal observations and relative stratigraphic position as biostratigraphic data to exactly constrain their ages is lacking; in calcareous nannofossil zone NN5 in the lower Badenian	Hladilová and Zdražílková (1989); Zágoršek (2010b)
Kroužek, Czech Republic	Carpathian Foredeep	15	Approximated from personal observations and relative stratigraphic position as biostratigraphic data to exactly constrain their ages is lacking; in calcareous nannofossil zone NN5 in the lower Badenian	Hladilová and Zdražílková (1989); Zágoršek (2010b)
Podbřežice, Czech Republic	Carpathian Foredeep	15	Presence of the foraminifera *Globigerinoides bisphericus* and *Praeorbulina glomerosa* in calcareous nannofossil zone NN5 indicates lower Badenian	Zágoršek and Holcová (2005); Zágoršek (2010a)
Szentkút, Hungary*	Nograd	15	Presence of foraminifera *Uvigerina macrocarinata* before FAD of *Orbulina* in calcareous nannofossil zone NN5 indicates lower Badenian	Holcová and Zágoršek (2007)
Hluchov, Czech Republic*	Carpathian Foredeep	16	Presence of foraminifera *Pararotalia canui* and *Pappina breviformis* in calcareous nannofossil zone NN4 indicates the lowermost Badenian	Zágoršek (2010b); Zágoršek et al. (2010)
Přemyslovice, Czech Republic	Carpathian Foredeep	16	Presence of foraminifera *Uvigerina macrocarinata* in calcareous nannofossil zone NN4 indicates the lowermost Badenian	Holcová et al. (2007); Zágoršek (2010b)
Brugg, Austria	Eastern Alpine Foredeep	18	We assign this locality to the lower Ottnangian regional stage based on its bivalves (probably *Pecten hermansenni*) and foraminifera as well as the lithostratigraphic correlation of this locality with the Zogelsdorf Formation	Jenke (1993); Piller et al. (2007)
Oberdürnbach, Austria*	Eastern Alpine Foredeep	18	We assign the Zogelsdorf Formation to the lower Ottnangian regional stage based on its pectinids, carbonate ecology, and sequence stratigraphy (i.e., there is a major unconformity below, and it interfingers with the Ottnangian aged Zellerndorf Formation)	Vávra (1987); Piller et al. (2007)

Correlations and numerical ages are from Piller et al. (2007, Fig. 1), Hohenegger et al. (2009, Fig. 2), and Kovácová et al. (2009, Fig. 2)
* Excluded from final analysis due to diagenetic alteration

Fig. 2 Early to Middle Miocene stratigraphic chart, showing stratigraphic position and oxygen isotope values (mean and range) of localities in this study relative to global oxygen isotope data of Zachos et al. (2001, Fig. 2) and to the calcareous nannofossil zones of Martini (1971). Modified from Hohenegger et al. (2009, Fig. 2) and Hohenegger and Wagreich (2012, Fig. 7)

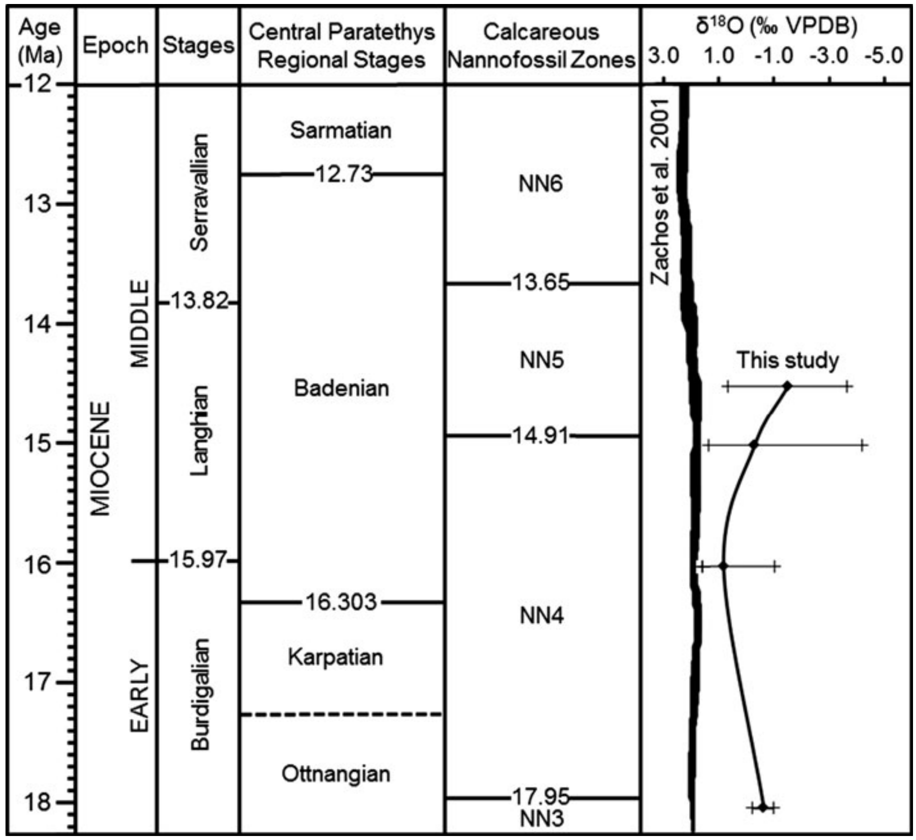

Table 2 Summary $\delta^{13}C$ and $\delta^{18}O$ statistics for each locality arranged by age from Table 1

Locality	*n*	$\delta^{13}C$ (‰ VPDB)			$\delta^{18}O$ (‰ VPDB)		
		Range	Mean	Standard deviation	Range	Mean	Standard deviation
Rauchstallbrunngraben*	6	−4.3 to −4.2	−4.25	0.03	−7.0 to −6.7	−6.79	0.12
Eisenstadt*	10	−6.0 to −4.6	−5.25	0.45	−5.4 to −3.6	−4.37	0.55
Niederleis	22	−2.2 to 1.8	0.11	1.28	−3.4 to 0.7	−1.04	1.23
Podbřežice Village	24	−1.2 to 0.8	−0.22	0.53	−3.7 to −0.5	−1.94	0.82
Steinebrunn*	5	−3.3 to 0.0	−2.02	1.66	−6.5 to −1.3	−3.84	2.31
Židlochovice	36	−2.0 to 1.0	−0.27	0.56	−4.2 to 1.4	−0.82	1.05
Holubice	64	−2.1 to 2.0	0.40	0.92	−2.4 to 1.3	−0.40	0.85
Kroužek	17	−1.1 to 2.5	1.17	0.90	−2.0 to −0.3	−1.01	0.54
Podbřežice	147	−2.2 to 1.8	0.97	0.55	−2.4 to 1.3	−0.05	0.62
Szentkút*	10	−2.2 to −1.2	−1.57	0.39	−4.7 to −2.7	−3.71	0.74
Hluchov*	14	−5.4 to −3.8	−4.78	0.48	−5.2 to −4.5	−4.97	0.22
Přemyslovice	12	−2.9 to −0.1	−1.79	0.84	−1.0 to 1.6	0.82	0.87
Brugg	16	−1.5 to −0.3	−0.82	0.35	−1.0 to −0.2	−0.64	0.23
Oberdürnbach*	16	−4.9 to −1.9	−3.95	1.01	−4.1 to −1.2	−3.14	0.94

* Excluded from final analysis due to diagenetic alteration

Results and discussion

A total of 399 samples were analyzed (Table 2) including bryozoans ($n = 353$), rock matrix ($n = 30$), and the large foraminifera *Amphistegina* ($n = 16$). The following cheilostomes were analyzed: *Cellaria*, *Celleporaria*, *Metrarabdotos*, *Myriapora*, *Reteporella*, and *Smittina*. The following cyclostomes were analyzed: *Crisidmonea*, *Exidmonea*, *Hornera*, *Mecynoecia*, *Pleuronea*, *Polyascosoecia*, and *Ybselosoecia*. $\delta^{13}C$ values ranged from −6.0 ‰

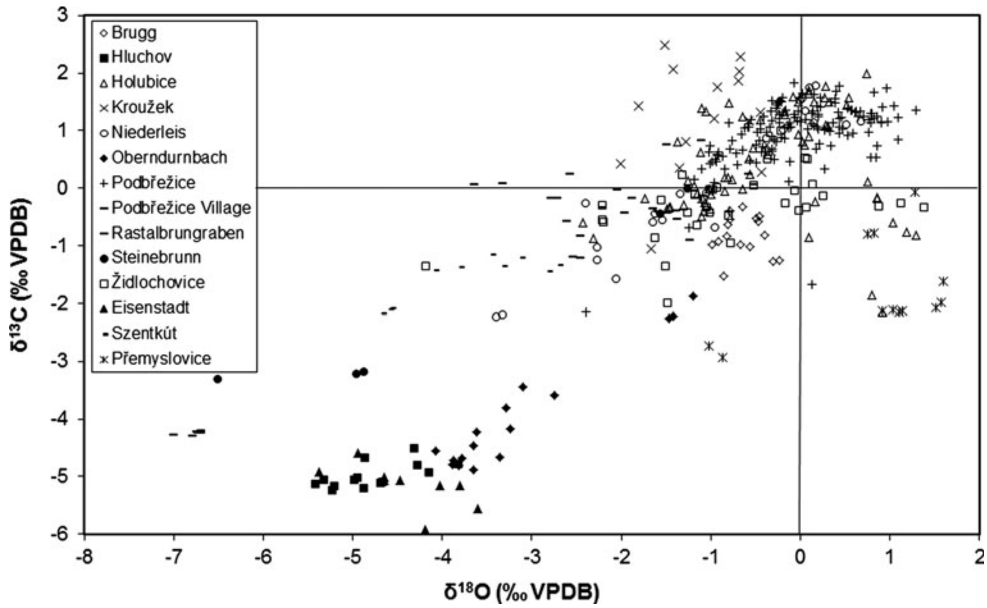

Fig. 3 $\delta^{18}O$ versus $\delta^{13}C$ plot of all 399 samples from all 14 localities. The six localities in the lower left quadrant with lower and covarying $\delta^{13}C$–$\delta^{18}O$ values with filled symbols (i.e., Eisenstadt, Hluchov, Oberdürnbach, Rauchstallbrunngraben, Steinebrunn, and Szentkút) were eliminated from the remaining analyses due to inferred diagenetic alteration

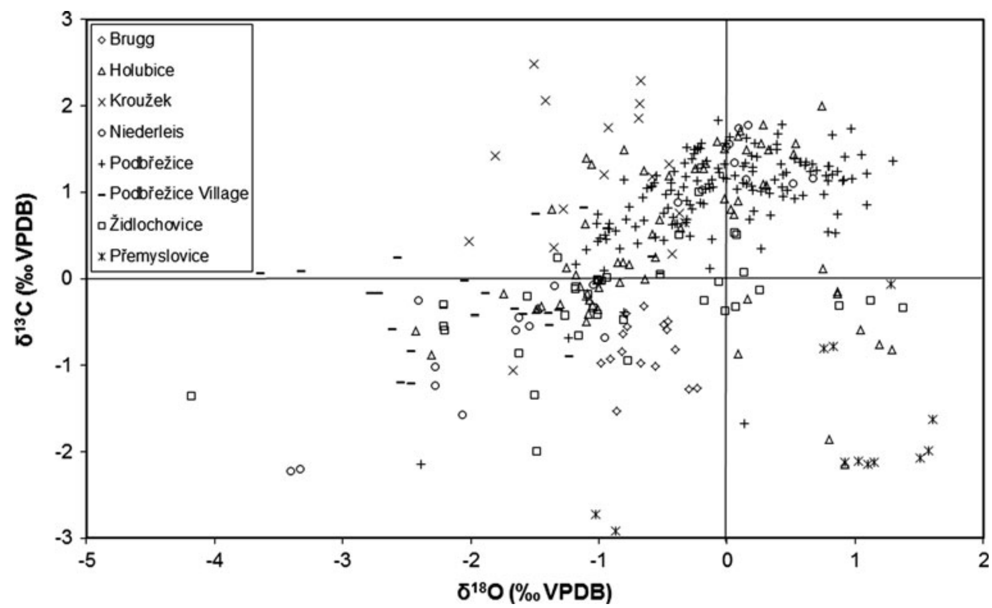

Fig. 4 $\delta^{18}O$ versus $\delta^{13}C$ plot of remaining 338 samples from eight localities interpreted to be less diagenetically altered

VPDB to 2.5 ‰ VPDB (mean = −0.2 ‰ VPDB, standard deviation = 1.9 ‰ VPDB). $\delta^{18}O$ values ranged from −7.0 ‰ VPDB to 1.6 ‰ VPDB (mean = −1.0 ‰ VPDB, standard deviation = 1.7 ‰ VPDB). The data show a series of six localities with values trailing off toward more negative $\delta^{13}C$ and $\delta^{18}O$ values (Fig. 3). The six localities are Rauchstallbrunngraben, Eisenstadt, Steinebrunn, Szentkút, Hluchov, and Oberdürnbach. In carbonate rocks, $\delta^{13}C$–$\delta^{18}O$ covariance is attributed to post-depositional diagenetic alteration by meteoric waters leading to lower $\delta^{13}C$ and $\delta^{18}O$ values (Veizer 1983; Marshall 1992). These six altered localities were significantly (t test, $p < 0.001$) lower on average in $\delta^{13}C$ (−3.8 ‰ VPDB) and $\delta^{18}O$ (−4.3 ‰ VPDB) than the presumed unaltered localities (0.4 ‰ VPDB and −0.4 ‰ VPDB, respectively).

The data from the six more diagenetically altered localities were excluded from future analyses leaving 338 samples (85 % of the original data set) from eight localities (Niederleis, Podbřežice Village, Židlochovice, Holubice, Kroužek, Podbřežice, Přemyslovice, and Brugg; Fig. 4) ranging in age from 14.5 to 18 Ma (Table 2). This same approach was used by Grunert et al. (2010) to exclude samples due to the influence of meteoric and pedogenic diagenesis as reflected in aberrantly low C and O isotope values (Armstrong-Altrin et al. 2009). The remaining localities included 298 bryozoan samples, 24 rock matrix samples, and 16 foraminifera samples. Our $\delta^{13}C$ and $\delta^{18}O$ values overlap nicely with the bryozoans analyzed by Holcová and Zágoršek (2008) as well as by Nehyba et al. (2008a) from the same sites.

There is a gradient between two end member localities (Table 2; Fig. 4). Kroužek is significantly (t test, $p < 0.001$) higher on average in $\delta^{13}C$ (1.2 ‰ VPDB) and lower on average in $\delta^{18}O$ (−1.0 ‰ VPDB) than Přemyslovice (mean = −1.8 ‰ VPDB and 0.8 ‰ VPDB, respectively). The other localities (e.g., Niederleis, Podbřežice Village, Židlochovice, Holubice, Podbřežice, and Brugg) are more intermediate.

Of the localities with intermediate isotope values between Přemyslovice and Kroužek, Niederleis stands out as the most variable (Table 2; Fig. 4). It has the highest combined coefficients of variation for $\delta^{13}C$ and $\delta^{18}O$ values (5.9 and 4.5, respectively). Such variability in stable isotope values from a single location could be due to either the degree of diagenesis as discussed earlier or the degree of paleoenvironmental variation in that locality due to shorter term time averaging/reworking or longer term temporal/stratigraphic variation.

We tested the shorter term time averaging/reworking scenario by comparing the isotope values of the bryozoan allochems and the rock matrix. There was no significant difference between the bryozoans and the rock matrix. Their $\delta^{18}O$ values (bryozoans: mean = −0.4 ‰ VPDB, standard deviation = 1.0 ‰ VPDB; matrix: mean = −0.5 ‰ VPDB, standard deviation = 0.8 ‰ VPDB) and $\delta^{13}C$ values (bryozoans: mean = 0.4 ‰ VPDB, standard deviation = 1.0 ‰ VPDB; matrix: mean = 0.5 ‰ VPDB, standard deviation = 1.4 ‰ VPDB) were not significantly different (t tests, $p > 0.05$) from those of the rock matrix. We interpret this to indicate the bryozoan allochems and the matrix formed in the same environment (e.g., Nehyba et al. 2008b) and there was minimal post-mortem transport of shallow water faunas to the deeper parts of basins (Roetzel and Pervesler 2004; Spezzaferri 2004). An alternative interpretation is that the bryozoan allochems and matrix underwent the same diagenetic alteration. We cannot rule this out completely other than by the earlier rejection of all the data from the localities whose isotope values indicated diagenesis.

This minimal mixing of environments before final deposition is typical of the middle Badenian bryoevent that was generally an autochthonous accumulation of bryozoan allochems with minimal transport distances (Zágoršek 2010a). Local changes in depth and/or salinity would also cause variation in isotope values, but they were probably of minimal impact on the bryozoans as only subtle changes in the bryozoan species associations occur through the bryoevent (Zágoršek and Holcová 2005; Zágoršek 2010a).

In contrast, there was a significant difference between the bryozoans and the foraminifera *Amphistegina*. *Amphistegina* is a shallow water large benthic foraminifera with symbiotic diatoms (Hallock 1999). Due to the vital effect of the symbionts, the tests of *Amphistegina* are calcified with increases in $\delta^{18}O$ of 0.2 ‰ PDB (Marques et al. 2007) to 0.8 ‰ PDB (Saraswati 2007). Our results ($n = 16$, $\delta^{18}O$ values: mean = −0.6 ‰ VPDB, standard deviation = 0.6 ‰ VPDB; $\delta^{13}C$ values: mean = 0.8 ‰ VPDB, standard deviation = 0.3 ‰ VPDB), indicate a mean increase of 0.4 ‰ VPDB for $\delta^{18}O$ and a mean decrease of 0.2 ‰ VPDB for $\delta^{13}C$ compared with the bryozoans. This foraminifera exhibits a significant vital effect compared with the bryozoans (t tests, $p < 0.05$ and $p < 0.001$, respectively).

The localities with intermediate isotope values between Přemyslovice and Kroužek such as Niederleis could reflect longer term temporal/stratigraphic variation in water depth, salinity and/or temperature. As is generally the case, the Miocene of the Central Paratethys was affected by a range of processes from global climate-induced sea level changes to regional tectonism-induced paleogeographic restructurings, which affected ocean circulation, salinity, and climate (Golonka et al. 2006). As outlined in the geologic setting and Early to Middle Miocene history above, there were significant regional paleoenvironmental fluctuations during this time involving changes in water depth/sea level, salinity, and temperature.

Changes in water depth/sea level

The localities with intermediate isotope values between Přemyslovice and Kroužek could reflect variations in water depth as there were global sea level changes during the Early to Middle Miocene. The various localities may represent different horizons within deepening or shallowing upward global sequences. The Badenian alone includes three third-order sea level sequences (Strauss et al. 2006; Piller et al. 2007). Harzhauser and Piller (2007) correlate these to the Ser1, Ser2, Ser3 European sequences of Hardenbol et al. (1998). Hohenegger et al. (2009) correlate them to the TB 2.3, 2.4, and 2.5 global sea level cycles of Haq et al. (1987). The Ottnangian represents another third-order sea level sequence (i.e., Haq et al.'s (1987) TB 2.1). All of our samples, except the oldest Ottnangian Brugg locality, were deposited within the lowermost Badenian transgression-regression cycle of Harzhauser and Piller (2007).

These global eustatic cycles are undoubtedly overprinted on top of tectonically controlled, more regional, sea level changes [e.g., Vienna Basin sea level cycles of Kováč et al. (2004)]. During Haq et al.'s (1987) TB 2.3 and 2.4 transgressions in the Langhian, tropical-subtropical water masses invaded the Central Paratethys (Rögl 1998). This was followed by decreasing sea level in response to global climatic cooling that has been attributed to the Middle Miocene climate transition (MMCT) at ~13.95 to 13.76 Ma (Zachos et al. 2001; Mourik et al. 2011). As this caused the main sea level induced decrease in water depth (i.e., the Mi-3b global cooling) and was younger than our samples, we rule out changes in water depth/sea level as a major source of variation in our isotope values.

In addition to these global or regional sea level changes over time, there were more localized, smaller variations in depth associated with a locality's position in its basin. For example, among some of our localities, based on foraminifera assemblages, there is a general shallowing gradient from Přemyslovice (interpreted as deepest; Zágoršek and Holcová 2009) to Szentkút (shallower; Moissette et al. 2007) and finally Eisenstadt (shallowest; Kroh et al. 2003). We choose not to put bathymetric ranges on these samples based on bryozoan assemblages as done by others (e.g., Moissette et al. 2007; Nehyba et al. 2008a) as the bathymetric ranges of the bryozoans in our study are not known except for *Smittina cervicornis* whose present-day known depth range is 30–120 m with a bathymetric optimum of 40–60 m (Moissette et al. 2007). In addition, these interlocality sources of variation, there may also reflect intralocality variation that our sampling cannot constrain.

Changes in salinity

The localities with intermediate isotope values between Přemyslovice and Kroužek could reflect variations in water salinity in response to changes in ocean circulation and stratification. The paleogeographic setting of the uplands (e.g., Bohemian massif, Calcareous Alps, and Western Carpathians) and the basins (Eastern Alpine Foredeep, Carpathian Foredeep, Vienna Basin, Eisenstadt Basin, Pannonian Basin, Nograd Basin) in the Central Paratethys (Fig. 1b) changed repeatedly during the Badenian (Piller et al. 2007). Decreasing sea level in response to global climatic cooling has been attributed to the MMCT at ~13.95 to 13.76 Ma (Zachos et al. 2001; Mourik et al. 2011). The dropping sea level caused a general trend of decreasing marine influence from more open marine circulation in the lower Badenian to more restricted circulation in the middle Badenian when net freshwater flow and oceanic inflow was exceeded by evaporation and resulted in increased stratification and the Badenian Salinity Crisis (BSC) around the NN5/NN6 transition zone associated with the upper part of the TB 2.5 sea level cycle (Jiménez-Moreno et al. 2005; Báldi 2006; Piller et al. 2007; Kováčová, et al. 2009). As the regional BSC began at 13.81 Ma (De Leeuw et al. 2010), after our samples were deposited, we rule out salinity change as a major source of variation in our isotope values.

Changes in temperature due to climate

The localities with intermediate isotope values between Přemyslovice and Kroužek could reflect variation in climatic conditions as there were major global climate changes during the Middle Miocene (Shackleton and Kennett 1975; Flower and Kennett 1994; Verducci et al. 2009). The Early/Middle Miocene Climatic Optimum (17–15 Ma) was the warmest period of the last 35 Myr (Zachos et al. 2001; Wan et al. 2009; You et al. 2009). This period was followed by a general cooling during the MMCT at ~15 to 13.7 Ma (Flower and Kennett 1994; Miller et al. 1991; Zachos et al. 2001; Lewis et al. 2007). The MMCT was widely recorded in the middle Badenian of the Paratethys area (Schwarz 1997; Vennemann and Hegner 1998; Gonera et al. 2000; Ivanov et al. 2002; Bicchi et al. 2003; Böhme 2003; Jiménez-Moreno et al. 2005; Báldi 2006; Harzhauser and Piller 2007), with the main period of change in the Central Paratethys dated to 13.95–13.76 Ma (Mourik et al. 2011). As the global MMCT occurred after our samples were deposited, we rule out climate change as a major source of variation in our isotope values.

Zachos et al.'s (2001) global O isotope curve (Fig. 2) indicates a relatively stable temperature during the period of our samples (i.e., 18–14.5 Ma). Zachos et al.'s (2001) $\delta^{18}O$ values are less variable than ours. This is because they are all from >1,000 m depth which is below the thermocline where water temperatures are less variable. Our $\delta^{18}O$ values are more variable because they are from shallow water in or above the thermocline and affected by seasonal upwelling as indicated below which can bring the thermocline almost to the surface (D'Croz and O'Dea 2007). Zachos et al.'s (2001) $\delta^{18}O$ values are more positive than ours. This is again because they are all from >1,000 m depth where water temperatures are lower than our shallow water environments. Regardless of these differences in the two data sets, the ages of our samples fall within the period of relatively warm and stable temperatures of the Early/Middle Miocene Climatic Optimum (Zachos et al. 2001; Wan et al. 2009; You et al. 2009). Thus our oxygen isotope curve correlates well with the Zachos et al. (2001) curve showing the Langhian/early Badenian warming trend which is the warmest Miocene climate period in the Central Paratethys.

Changes in temperature due to upwelling

As we have argued against the isotopic effects of global and/or regional changes in sea level, salinity, and climate, we therefore attribute the isotope values from the bryozoans to localized upwelling. Surface waters in upwelling areas show a characteristic isotopic signal. Using recent molluscs, Killingley and Berger (1979) were the first to use stable isotopes to test for upwelling conditions. Their study showed that organisms which calcify in an upwelling environment yield higher δ^{18}O values and lower δ^{13}C values. Other studies have shown this with recent and fossil foraminifera (e.g., Faul et al. 2000; Peeters et al. 2002). Upwelling causes higher δ^{18}O values in response to mixing with upwelled deeper, colder waters. The corresponding upwelling-induced lower δ^{13}C values result from mixing with upwelled deeper, more nutrient-rich waters containing older dissolved inorganic carbon with low δ^{13}C values (Steens et al. 1992; Wefer et al. 1999; Peeters et al. 2002). The higher nutrient availability causes faster calcification at a higher respiration rate, which involves more respired CO_2 with lower δ^{13}C values (Wurster and Patterson 2003; Naidu and Niitsuma 2004).

Our bryozoan samples had a mean δ^{13}C value of 0.4 ‰ (n = 298, range: −2.2 to 2.5 ‰, standard deviation = 1.0 ‰) which is lower than the range in mean global values from 18 to 14 Ma of 1.0 to 1.9 ‰ (Zachos et al. 2001). Our bryozoan samples had a mean δ^{18}O value of −0.4 ‰ (n = 298, range: −4.2 to 1.6 ‰, standard deviation = 1.0 ‰) which is lower than the range in mean global values from 18 to 14 Ma of 1.6 to 1.9 ‰ (Zachos et al. 2001). Thus, the δ^{13}C results support upwelling. The δ^{18}O values do not show the predicted higher values as our samples are from shallow water, whereas Zachos et al.'s (2001) are from colder deep-sea environments (i.e., >1,000 m depth). We interpret the higher δ^{13}C and lower δ^{18}O values in Kroužek as indicative of warmer surface waters, whereas the lower δ^{13}C and higher δ^{18}O values in Přemyslovice are interpreted as mixing with upwelled deeper, colder, more nutrient-rich waters. Grunert et al. (2010) used isotope data from foraminifera to argue for upwelling in the Central Paratethys during the Early Miocene. Our results fall within their range of upwelling areas (i.e., δ^{13}C: −3.0 to 0.5 ‰, δ^{18}O: −2.5 to 0.5 ‰).

In addition to Grunert et al. (2010), the presence of upwelling in the Central Paratethys from the Ottnangian to Badenian has been suggested by other authors. Ćorić and Rögl (2004) attributed the distribution of calcareous nannofossils in the Alpine-Carpathian Foredeep during the early Badenian to upwelling. Roetzel et al. (2006) used foraminifera assemblage compositions to infer upwelling in this same area in the Early Miocene. Most importantly to this study, Zágoršek (2010b) used changes in the bryozoan species associations and δ^{13}C values from bryozoans to similarly infer the role of upwelling in the creation of the Badenian bryoevent in the Central Paratethys.

Experiments using a global ocean general circulation model have shown that the paleolatitude and longitude of the general region of the Central Paratethys should have experienced high rates of wind-driven upwelling of relatively cold and deep water through the Miocene (Hotinski and Toggweiler 2003). Today, Přemyslovice is located 60 km northeast of Kroužek which would have put it in a more restricted part of the Carpathian Foredeep where it would have been more susceptible to upwelling from the dominant northwesterly winds than Kroužek which was located more in the center of the Carpathian Foredeep (Fig. 1b). The dominant wind direction is from the northwest to the southeast at this latitude (i.e., ~45°N) today. Despite the different paleoenvironmental setting in the Miocene, the paleolatitude was similar to today (Blakey 2011). This places the Carpathian Foredeep in the westerlies wind belt. For example, the most common wind direction today in Brno, Czech Republic (36 % of time) is out of the northwest (Windfinder.com 2011). That would suggest upwelling along the northwest margin of the Carpathian Foredeep. It is possible that the Carpathian Foredeep was oriented more east–west during the Badenian (e.g., reconstructions by Jiménez-Moreno et al. 2005, Fig. 2; Golonka et al. 2006, Fig. 20) than its more northeast-southwest orientation today (Fig. 1b). There could also have been upwelling along the northern margin of an east–west oriented Carpathian Foredeep if the dominant winds were out of the west as they could cause upwelling due to the Coriolis Effect as suggested by Grunert et al. (2010, Fig. 10A) for the Central Paratethys in the Early Miocene. This is supported by the fact that in Brno, Czech Republic the wind blows out of the west 34 % of the time (Windfinder.com 2011). In addition to wind patterns, coastal upwelling can also be induced by tidal currents (e.g., Lee et al. 1997) and topography (e.g., Oke and Middleton 2000) as suggested by Grunert et al. (2010) in their analysis of upwelling conditions in the Early Miocene Central Paratethys Sea. It is presumed that the seasonally upwelled water ultimately warms and mixes with adjacent surface waters and loses its identity (Richards 1981).

In addition, the regional upwelling situation may have been complicated by the global stepwise cooling between 15 and 10 Ma (Zachos et al. 2001) which caused a southward shift of the boundary between the westerlies and the trade winds in the northern hemisphere (Böhme 2004). This is reflected in the regional distribution of 16–14.5 Ma volcanic ash deposits (Rocholl et al. 2008) and 14.7–14.5 Ma ectothermic vertebrates (Böhme 2003) which suggest more easterly stratospheric winds in the European mid-latitudes, but only during the summer season (Rocholl et al. 2008). The existence of regional upwelling has been supported empirically by benthic and planktonic microfossil assemblages from the Alpine-Carpathian Foredeep in the Early and Middle Miocene (Ćorić and Rögl 2004; Grunert et al. 2010), the same ages as our localities. As the main cooling event occurred in the Central Paratethys from 13.95 to 13.76 Ma (Mourik et al. 2011), any potential effect of shifting trade winds probably happened after the samples in this study were deposited.

Paleotemperatures

To calculate paleotemperatures from δ^{18}O values, we used Kim and O'Neil's (1997) calcite equation on all the samples except for the aragonitic *Smittina* colonies (Smith et al. 2006). For those, we used Patterson et al.'s (1993) aragonite equation. In case some of the *Smittina* colonies were primarily calcite as opposed to aragonite (e.g., the European *S. messiniensis* in Berning 2006), we also calculated their temperatures using the above calcite equation. These equations require knowing the δ^{18}O value for the seawater in which the bryozoans grew. By definition, today's Standard Mean Ocean Water (SMOW) has a mean δ^{18}O composition of 0 ‰. The δ^{18}O value of seawater varies over time due to global changes in terrestrial ice volume (Shackleton 1987) and local/regional changes in salinity in response to evaporation and mixing with freshwater (Delaygue et al. 2001). Lear et al. (2000) estimated that the global δ^{18}O seawater values for the Early to Middle Miocene varied between −0.2 and −0.8 ‰. Similarly Zachos et al. (2001) argued that δ^{18}O values for seawater typically varied between 0 and −1 ‰ in normal marine conditions during glacial and interglacial Miocene periods, respectively. Locally, evaporation may increase δ^{18}O seawater values, if it has a longer residence time in hydrologically more restricted basins (Swart et al. 1989). Thus, higher salinities result in higher δ^{18}O seawater values which yield higher paleotemperatures. Restricted marine environments such as the Central Paratethys are susceptible to these salinity fluctuations. Reichenbacher et al. (2004) found this to be true in the Paratethyan Early Miocene Northern Alpine Basin in Germany. The same is true today as the Mediterranean Sea has a value of +1 ‰, the more saline Red Sea around +2 ‰, and the more brackish Black Sea −3 ‰ (Latal et al. 2006). Previous studies in the same general region of the Central Paratethys during roughly the same stratigraphic interval can help constrain our δ^{18}O values for seawater.

Hladilová et al. (1998) assumed a δ^{18}O value for seawater of 0 ‰ for their study of Badenian molluscs from the Vienna Basin in Slovakia. Gonera et al. (2000) used the same value for Badenian foraminifera from the Carpathian Foredeep in Poland. Bojar et al. (2004) chose seawater δ^{18}O values of −0.1 and −0.7 ‰ for their Styrian Basin, Austria study of early Badenian molluscs and brachiopods, respectively. Latal et al. (2006) took a more cautious approach in their study of early Badenian molluscs from the Northern Alpine Foreland Basin and used three different seawater δ^{18}O values to bracket their calculated paleotemperatures: +1.0, 0.0, and −1.0 ‰. Kováčová and Hudáčková (2009) used a seawater δ^{18}O value of −0.5 ‰ in their study of late Badenian foraminifera from the Vienna Basin, Slovakia. Kováčová et al. (2009) assumed a seawater δ^{18}O value of 0 ‰ for their study of Badenian foraminifera from the Vienna Basin, Slovakia.

Based on these previous studies, we decided to take the more prudent approach and bracket the δ^{18}O values for seawater from +1.0 to −1.0 ‰. Using the δ^{18}O results from only the bryozoan allochems, the calculated mean water temperatures ranged from 12 to 21 °C (midpoint = 16 °C, maximum range: 2–40 °C, standard deviation = 4.5 °C). Assuming all the *Smittina* colonies were calcite did not change the results significantly (i.e., range: 11–21 °C and no change in midpoint or maximum range). These values are higher than those reported in Gonera et al.'s (2000) study which calculated 6–11 °C from Badenian foraminifera from Poland in the Carpathian Foredeep of the Central Paratethys. The warmer, bryozoan-based paleotemperatures from this study are to be expected as the paleolatitude of the Polish part of Carpathian Foredeep is further north, but more importantly, Gonera et al.'s (2000) results are probably too low as the basin contained subtropical sirenians, foraminifera, bryozoans, etc. In contrast to Gonera et al. (2000), our results generally overlap with those of other studies. Hladíková and Hamršmíd (1986) calculated temperatures of 9–18 °C from lower Badenian fossils and sediments from the Carpathian Foredeep, Moravia, Czech Republic. Hladilová et al. (1998) examined Badenian mollusc isotopes from the Vienna Basin, Slovakia and calculated a temperature of 15 °C. Bojar et al. (2004) used isotopes from molluscs and brachiopods from the early Badenian of the Styrian Basin, Austria and calculated temperatures of 13–26 °C. Latal et al. (2006) studied early Badenian Northern Alpine Foreland Basin molluscs and calculated a range of 4–28 °C. Kováčová and Hudáčková's (2009) analysis of late Badenian foraminifera from the Vienna Basin yielded paleotemperatures of 9–20 °C. Kováčová et al. (2009) calculated paleotemperatures of 11–19 °C in their study of Badenian foraminifera from the Vienna Basin, Slovakia. Thus, the bryozoan colonies are yielding comparable results (12–21 °C) as other allochems.

Conclusions

Bryozoans, foraminifera, and rock matrix samples from 14 localities yielded 399 δ^{13}C and δ^{18}O values. The samples with outlier values from six localities (15 % of the total samples) were discarded due to diagenesis. The isotope values from individual bryozoan colonies were not significantly different from the matrix samples. We interpreted this to indicate minimal post-mortem transport of the bryozoan allochems. The isotope values from individual bryozoan colonies were significantly different from the *Amphistegina* samples. We interpreted this to indicate a vital effect present in the foraminifera.

The isotope values from the bryozoans were attributed primarily to localized upwelling as upwelling best explains the C and O isotope values. The isotopic effects of global and/or regional changes in sea level, salinity, and climate associated with the Middle Miocene climate transition were ruled out as they occur stratigraphically above our samples. Paleotemperatures for the Early to Middle Miocene sediments of the Central Paratethys were calculated at 12–21 °C. Despite potential taxonomic and diagenetic problems, bryozoan colonies are a powerful, underutilized source of paleoenvironmental C and O isotope data.

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