

Stable isotope composition of the Miocene Dinaride Lake System deduced from its endemic mollusc fauna

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Abstract The aragonite shells of 55 mollusc specimens from the late Early and early Middle Miocene of two palaeolakes of the Dinaride Lake System (DLS) are analysed for their $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures. The data set has a bimodal distribution with a prominent peak between -3 and -4‰ for both isotopes and a second much weaker peak at more depleted values of c. -9 to -7‰ . Taxa with ‘heavy’ values are interpreted to represent the inhabitants of the shores or shallow areas of the lake. Depleted

values are attributed to species preferring freshwater habitats of springs or small rivulets, thus representing the freshwater end-member. The overall rather high values in both stable isotopes result from a combination of evaporation effects and the influx of already isotopically heavy freshwater from the karstic catchment area. Thus, the DLS is interpreted as a closed freshwater system without marine influence but with enough contribution of freshwater to keep the oxygen values close to -5‰ . Mean lake surface water temperatures, based on the $\delta^{18}\text{O}_{\text{shell}}$ values, excluding the freshwater end-member taxa, range around roughly 19 – 21°C . Despite the problems in calculating these temperatures, the values are in agreement with mean annual air temperatures deduced from the palaeobotanic record by applying the Coexistence Approach method. The seasonal range was around 10 – 11°C and is mainly recorded in shells from lake settings. Taxa with freshwater end-member signatures lack this range due to the more stable temperature regime and less fluctuating dissolved inorganic carbon (DIC) pool. Congeneric species from the same stratigraphic horizon often display discrete but different isotope signatures. This fact suggests habitat segregation and might be a major factor for sympatric speciation and the endemic radiation within the mollusc fauna of the DLS.

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Introduction

The Dinaride Lake System (DLS) was a huge Miocene wetland system extending over an area of c. 75,000 km², consisting of several palaeolakes. The deposits of the DLS cover parts of Croatia, Bosnia and Herzegovina, Montenegro, Serbia, Hungary and Slovenia (Krstić et al., 2003). It harboured a diverse and fully endemic mollusc fauna which was described largely already in the nineteenth century (Harzhauser & Mandić, 2008). Despite its size and the importance of the mollusc fauna, the DLS gained surprisingly little attention by the scientific community. A poorly resolved stratigraphy and the unclear relations to other Miocene and Pliocene faunas might have been main reasons for this low interest. Important contributions by Mandić et al. (2009), Jiménez-Moreno et al. (2008, 2009) and de Leeuw et al. (2010) improved the stratigraphic correlations, clarified the absolute ages of important sections and provided data on sedimentary environments and palaeoclimate. One of the remaining problems in the DLS is its water chemistry (Krstić et al., 2003; Hajek-Tadesse et al., 2009).

Apparent similarities in taxonomic composition and evolutionary patterns with the much younger Late Miocene Lake Pannon suggest comparable environmental conditions (Harzhauser & Mandić, 2008, 2010). In particular, Early and Middle Miocene faunas of the DLS components Lake Sinj and Lake Drniš bear several taxa which are morphologically reminiscent of Late Miocene dreissenid and melanospid species from Lake Pannon. Stable isotope studies on Lake Pannon molluscs suggested that Lake Pannon was a slightly alkaline and brackish lake (Harzhauser et al., 2007a, b). Therefore, it was tempting to assume similar water chemistry for the Dinaride Lake System. Hypothetically, slight marine influx from the Adriatic Sea or contributions by Permian evaporites (Šušnjara & Sakač, 1988) could have played a role for brackish water conditions.

Herein, we focus on the stable isotope signatures (oxygen, carbon) of representative mollusc species to shed light on the water geochemistry of the DLS. The selected taxa represent different feeding strategies and ecological guilds. Based on the environmental requirements of modern relatives, these taxa are also suggested to have preferred different habitats within the lake. The data will thus document the overall isotope signature of the DLS.

Geological setting

The sampled localities are situated in the Sinj and Drniš basins which are two Dinaride intramontane basins (Korbar, 2009), situated in two karst poljes of 380 m mean topographic elevation (Fig. 1). They are tectonically disjoined by the 1,508 m high, NW–SE striking Mt. Svilaja. The latter is composed by Triassic to Cretaceous platform carbonates representing the NE margin of both basins (Ivanović et al., 1977; Papeš et al., 1984; Raić et al., 1984). Their SE margin comprises a series of Upper Cretaceous to Middle Eocene platform carbonates, Middle Eocene Flysch successions and Upper Eocene to Lower Oligocene Molasse deposits including conglomerates and paralic coal intercalations (Babić & Zupanič, 2007).

The basins belong to the main Dinaride wrenching zone of the Karlovac–Split suture (Schmid et al., 2008) and are related to Early to Middle Miocene transpressional tectonics, resulting from N-ward oblique-slip motions of the underthrusting Adriatic block (Tari, 2002). This event triggered formation of numerous related and synchronous NW–SE striking, restricted pull apart basins, distributed across the Dinarides and the southern Pannonian Basin. Therein, a mosaic freshwater system developed which is termed the Dinaride Lake System (Krstić et al., 2003; Harzhauser & Mandić, 2008). The studied samples, originating from two closely related palaeolakes of the DLS-SE margin, are located today between 25 and 43 km N from the Mediterranean harbour town Split in SE Croatia (Fig. 1). Whereas Lake Sinj was moderately sized with 140 km² surface area, Lake Drniš was rather small with a surface area of only 25 km². The latter estimate is, however, based on sediment distribution and considering its squeezed tectonic position the original size was certainly larger. The faunal composition of the two basins is similar but not completely identical (Brusina, 1884). As their synchronicity is indicated by similar taxa together with corresponding lithological features they rather did not belong to the same lake but were only in temporary connection (Jurišić-Polšak, 1999). Furthermore, the tectonic setting points to post-depositional transpression that shifted the basins into a closer position to one other. The initial transtensional regime caused massive gypsum doming from the basement horizon (Mandić et al., 2009). The gypsum originates from Permian shales representing the main Dinaride thrust belt

Fig. 1 Geographic and geologic overview of the study area. *Dark shaded areas* represent sediment distributions of the Dinaride Lake System. Compiled after geologic maps of former Yugoslavia 1:100,000 and 1:500,000 and ESRI ArcGIS base maps



decollement horizon (Tari, 2002). In both studied basins, this gypsum underlies directly the basal lake sediments (Ivanović et al., 1977; Šušnjara & Sakač, 1988).

The age of the fauna

The lacustrine series of the Sinj Basin was currently dated at the Lučane section by means of integrated

Ar/Ar geochronology and magnetostratigraphy (de Leeuw et al., 2010). This study revealed Lake Sinj as a long-lived palaeolake persisting about 3 My between 18 and 15 Ma. The absolute dating allows a very precise estimation of the age of the studied fauna, collected by Kittl (1895) at 5 localities: Miočić A ($16^{\circ}13'44,308''E$ $43^{\circ}52'35,793''N$) and Miočić B ($16^{\circ}13'14,948''E$ $43^{\circ}52'37,267''N$) in the Drniš Basin and Lučane ($16^{\circ}35'25,572''E$ $43^{\circ}43'11,317''N$),

Stuparuša (16°37'25,937"E 43°42'18,336"N) and Ribarić (16°32'19,187"E 43°49'9,144"N) in the Sinj Basin (Fig. 1). Only the Lučane locality provides a long section which is still accessible and described in detail in Mandić et al. (2009) and de Leeuw et al. (2010). The other localities are already inaccessible (e.g. Ribarić) or restricted to very poor and abandoned outcrops (e.g. Miočić). Therefore, no lithological logs can be provided for Miočić, Ribarić and Stuparuša.

The assemblage with *Prososthenia schwarzi* (Neumayr, 1875) occurs at the Lučane section in the uppermost lignite which is intercalated in a limestone series (Jiménez-Moreno et al., 2008; Mandić et al., 2009). It starts above the ash layer dated with 15.43 ± 0.05 Ma and is restricted to the time interval between 15.4 and 15.0 Ma (de Leeuw et al., 2010). The same assemblage is present in similar depositional settings and a coeval stratigraphic horizon at Ribarić (Kittl, 1895; Kerner, 1905a, b; Jurišić-Polšak, 1999). In contrast, Stuparuša, characterised by occurrence of *Melanopsis bicoronata* Brusina, 1884, has been shown by Kerner (1905a, b) to represent a slightly older stratigraphic horizon which is dated at the Lučane section to range between 16.8 and 16.6 Ma (de Leeuw et al., 2010).

Locality Miočić in the Drniš Basin comprises two horizons (Brusina, 1884; Kittl, 1895). Miočić A corresponds to fossil-rich bed with *Melanopsis inconstans* Neumayr, 1869 found in a distinct stratigraphic horizon of the Sinj Basin described by Kerner (1905a, b) as zone VIII and correlating to the Lučane time interval of 15.4–15.0 Ma. Miočić B represents a stratigraphically younger horizon with *Unio rackianus* Brusina, 1874 and *Bythinia jurinaci* (Brusina, 1902) (see Kittl, 1895). Its exact age, except for being younger than 15.0 Ma, is currently unknown.

Materials and methods

Shells of 55 mollusc specimens of 31 species have been analysed for oxygen and carbon isotopes, yielding 164 data-pairs (Table 1). Only pristine aragonite shells were sampled (except for *Theodoxus* which has traces of calcite). For stable isotope analyses, the shells were sampled with a 0.3-mm drill. Depending on shell size, the number of samples per shell ranges from 1 to 27. Total shell analysis has been performed on very small

shells, such as *Orygoceras* (marked by the appendix G in sample numbers in Table 1). The main scope of these measurements was to achieve a characteristic spectrum of isotope values, represented by the DLS molluscs. Therefore, only few specimens were sclero-chronologically analysed to receive data on seasonality. Oxygen and carbon isotopes were determined by reaction of the samples with 100% phosphoric acid at 70°C in a Finnigan Kiel II automated reaction system, and measured with a Finnigan Delta Plus isotope-ratio mass spectrometer at the Institute of Earth Sciences, University of Graz. Measurements of NBS-19 and an internal laboratory standard yielded a standard deviation of 0.1‰ for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Isotope data are given in ‰ relative to VPDB.

To cover a wide range of palaeolake environments, the samples were taken from very different taxa (numbers in parenthesis after the species indicate the numbers of specimens and the number of samples): 2 species of the family Neritidae: *Theodoxus lorkovici* (Brusina, 1878) ($n = 1/6$) and *Theodoxus semidentatus* (Sandberger, 1874) ($n = 1/5$); 11 species of the family Melanopsidae: *Melanopsis acanthica* Neumayr, 1869 ($n = 1/13$), *M. bicoronata* Brusina, 1884 ($n = 1/4$), *M. inconstans* Neumayr, 1869 ($n = 1/3$), *M. lanzaeana* Brusina, 1874 ($n = 1/5$), *M. lyrata* Neumayr, 1869 ($n = 1/8$), *M. panciciana* Brusina, 1874 ($n = 1/10$), *M. plicatula* Brusina, 1874 ($n = 1/6$), *M. sinjana* Brusina, 1874 ($n = 1/3$), *M. trstenjaki* Brusina, 1884 ($n = 1/1$), *M. visianiana* Brusina, 1874 ($n = 1/7$) and *M. zitteli* Neumayr, 1869 ($n = 1/27$); 1 species of the family Bithyniidae *Bithynia jurinaci* (Brusina, 1902) ($n = 3/5-3-1$); 13 species of the family Hydrobiidae *Prososthenia candidula* Neumayr, 1869 ($n = 5/1-1-1-1-1$), *Prososthenia cincta* Neumayr, 1869 ($n = 5/3-2$), *Prososthenia dalmatina* (Neumayr & Paul, 1875) ($n = 2/1-1$), *Prososthenia eburnea* Brusina, 1884 ($n = 2/1-1$), *Prososthenia neutra* Brusina, 1897 ($n = 2/2$), *Prososthenia schwarzi* (Neumayr & Paul, 1875) ($n = 5/1-1-1-1-1$), *Prososthenia tournoueri* (Neumayr, 1869) ($n = 2/1-1$), *Fossarulus moniliferus* Brusina, 1876 ($n = 2/1-1$), *Fossarulus tricarinatus* Brusina, 1870 ($n = 1/1$), *Pseudamnicola torbariana* Brusina, 1874 ($n = 3/1-1-1$); *Emmericia canaliculata* Brusina, 1870 ($n = 2/1-1$), *Dianella haueri* (Neumayr, 1869) ($n = 2/6-1$), and 2 Planorbidae species *Orygoceras cornucopiae* Brusina, 1882 ($n = 3/1-1-1$) and *Orygoceras dentaliforme* Brusina, 1882 ($n = 3/1-1-1$). Only two bivalves have been

Table 1 Data sheet of all measured specimens (isotope data are given in ‰ relative to VPDB)

No.	Locality	Genus	Species	Sample code	d18O	d13C
1	Miočić A	<i>Orygoceras</i>	<i>cornucopiae</i>	M1_Oryg_cornu_A-G	-6.633	-6.782
2	Miočić A	<i>Orygoceras</i>	<i>cornucopiae</i>	M1_Oryg_cornu_B-G	-7.763	-8.367
3	Miočić A	<i>Orygoceras</i>	<i>cornucopiae</i>	M1_Oryg_cornu_C-G	-1.674	-3.719
4	Miočić A	<i>Theodoxus</i>	<i>lorkovici</i>	M1_Theo_lork_A1	-7.313	-6.553
4	Miočić A	<i>Theodoxus</i>	<i>lorkovici</i>	M1_Theo_lork_A2	-7.31	-6.302
4	Miočić A	<i>Theodoxus</i>	<i>lorkovici</i>	M1_Theo_lork_A3	-7.714	-6.664
4	Miočić A	<i>Theodoxus</i>	<i>lorkovici</i>	M1_Theo_lork_A4	-7.729	-6.809
4	Miočić A	<i>Theodoxus</i>	<i>lorkovici</i>	M1_Theo_lork_A5	-7.592	-6.719
4	Miočić A	<i>Theodoxus</i>	<i>lorkovici</i>	M1_Theo_lork_A6	-7.693	-7.022
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_1	-7.801	-5.148
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_2	-6.475	-5.467
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_3	-7.748	-5.335
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_4	-7.04	-6.322
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_5	-7.11	-6.455
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_6	-5.5	-6.441
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_7	-7.222	-6.108
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_8	-7.197	-5.7
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_9	-7.632	-5.256
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_10	-6.567	-6.278
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_11	-6.868	-5.649
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_12	-7.123	-4.488
5	Miočić A	<i>Melanopsis</i>	<i>acanthica</i>	M1_Mela_acan_13	-7.094	-5.641
6	Miočić A	<i>Melanopsis</i>	<i>inconstans</i>	M1_Mela_inco_A1	-3.301	-4.321
6	Miočić A	<i>Melanopsis</i>	<i>inconstans</i>	M1_Mela_inco_A2	-4.149	-4.893
6	Miočić A	<i>Melanopsis</i>	<i>inconstans</i>	M1_Mela_inco_A3	-2.079	-4.63
7	Miočić A	<i>Melanopsis</i>	<i>plicatula</i>	M1_Mela_plic_A1	-3.194	-4.57
7	Miočić A	<i>Melanopsis</i>	<i>plicatula</i>	M1_Mela_plic_A2	-1.980	-3.566
7	Miočić A	<i>Melanopsis</i>	<i>plicatula</i>	M1_Mela_plic_A3	-1.665	-3.488
7	Miočić A	<i>Melanopsis</i>	<i>plicatula</i>	M1_Mela_plic_A4	-2.813	-3.323
7	Miočić A	<i>Melanopsis</i>	<i>plicatula</i>	M1_Mela_plic_A5	-3.193	-2.905
7	Miočić A	<i>Melanopsis</i>	<i>plicatula</i>	M1_Mela_plic_A6	-3.395	-3.561
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A1	-5.261	-2.444
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A2	-5.595	-4.107
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A3	-5.472	-4.729
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A4	-3.617	-1.999
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A5	-5.041	-4.685
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A6	-4.687	-4.547
8	Miočić A	<i>Melanopsis</i>	<i>visianiana</i>	M1_Mela_visi_A7	-4.049	-2.945
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_1	-3.772	-3.806
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_2	-3.279	-3.407
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_3	-4.777	-4.029
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_4	-3.357	-3.471
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_5	-4.76	-3.751
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_6	-3.807	-3.257

Table 1 continued

No.	Locality	Genus	Species	Sample code	d18O	d13C
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_7	-4.337	-3.326
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_8	-3.439	-3.943
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_9	-3.504	-3.093
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_10	-3.108	-3.478
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_11	-3.123	-2.891
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_12	-4.504	-3.548
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_13	-4.486	-3.927
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_14	-4.318	-3.933
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_15	-2.95	-3.358
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_16	-2.596	-2.845
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_17	-4.378	-3.922
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_18	-4.2	-3.066
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_19	-4.909	-4.302
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_20	-4.804	-4.124
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_21	-4.631	-3.975
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_22	-4.561	-4.216
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_23	-4.026	-4.565
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_24	-3.069	-4.786
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_25	-3.236	-5.25
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_26	-3.735	-5.491
9	Miočić A	<i>Melanopsis</i>	<i>zitteli</i>	M1_Mela_zitt_27	-4.079	-4.279
10	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_A1	-6.979	-8.552
10	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_A2	-7.505	-8.137
10	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_A3	-7.416	-8.158
10	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_A4	-7.256	-8.437
10	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_A5	-6.761	-8.863
10	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_A6	-7.074	-8.416
11	Miočić A	<i>Dianella</i>	<i>haueri</i>	M1_Pyrg_haue_B-G	-6.610	-8.919
12	Miočić A	<i>Prososthenia</i>	<i>eburnea</i>	M1_Pros_ebur_A-G	-6.532	-4.868
13	Miočić A	<i>Prososthenia</i>	<i>eburnea</i>	M1_Pros_ebur_B-G	-5.487	-5.209
14	Miočić A	<i>Prososthenia</i>	<i>neutra</i>	M1_Pros_neut_A-G	-4.976	-4.603
15	Miočić A	<i>Prososthenia</i>	<i>neutra</i>	M1_Pros_neut_B-G	-6.072	-7.589
16	Miočić A	<i>Prososthenia</i>	<i>tournoueri</i>	M1_Pros_tour_A1	-8.48	-7.627
17	Miočić A	<i>Prososthenia</i>	<i>tournoueri</i>	M1_Pros_tour_B-G	-7.759	-8.173
18	Miočić A	<i>Bithynia</i>	<i>jurinaci</i>	M1_Byth_juri_A1	-3.913	-6.395
18	Miočić A	<i>Bithynia</i>	<i>jurinaci</i>	M1_Byth_juri_A2	-4.662	-6.547
18	Miočić A	<i>Bithynia</i>	<i>jurinaci</i>	M1_Byth_juri_A3	-3.713	-6.569
18	Miočić A	<i>Bithynia</i>	<i>jurinaci</i>	M1_Byth_juri_A4	-3.886	-6.015
18	Miočić A	<i>Bithynia</i>	<i>jurinaci</i>	M1_Byth_juri_A5	-3.260	-6.886
19	Miočić A	<i>Prososthenia</i>	<i>dalmatina</i>	M1_Lito_dalm_A-G	-3.857	-4.507
20	Miočić A	<i>Prososthenia</i>	<i>dalmatina</i>	M1_Lito_dalm_B-G	-2.714	-5.402
21	Miočić B	<i>Emmericia</i>	<i>canaliculata</i>	M2_Emer_cana_A-G	-6.43	-9.233
22	Miočić B	<i>Emmericia</i>	<i>canaliculata</i>	M2_Emer_cana_B-G	-5.132	-8.068
23	Miočić B	<i>Pseudoamnicola</i>	<i>torbariana</i>	M2_Pseu_torb_A-G	-1.556	-4.269

Table 1 continued

No.	Locality	Genus	Species	Sample code	d18O	d13C
24	Miočić B	<i>Pseudoamnicola</i>	<i>torbariana</i>	M2_Pseu_torb_B-G	-1.862	-8.98
25	Miočić B	<i>Pseudoamnicola</i>	<i>torbariana</i>	M2_Pseu_torb_C-G	-1.679	-7.563
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_1	-2.491	-8.372
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_2	-2.934	-7.72
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_3	-3.478	-5.956
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_4	-3.412	-5.852
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_5	-3.155	-6.534
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_6	-3.617	-6.129
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_7	-3.355	-6.237
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_8	-3.652	-6.156
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_9	-3.201	-6.695
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_10	-3.653	-7.722
26	Miočić B	<i>Unio</i>	<i>rackianus</i>	M2_Unio_rack_11	-3.64	-8.237
27	Miočić B	<i>Bithynia</i>	<i>jurinaci</i>	M2_Byth_turi_A1	-2.832	-7.726
27	Miočić B	<i>Bithynia</i>	<i>jurinaci</i>	M2_Byth_turi_A2	-3.028	-7.693
27	Miočić B	<i>Bithynia</i>	<i>jurinaci</i>	M2_Byth_turi_A3	-2.919	-8.28
28	Miočić B	<i>Bithynia</i>	<i>jurinaci</i>	M2_Byth_turi_B-G	-4.682	-9.301
29	Lučane	<i>Melanopsis</i>	<i>trstenjaki</i>	L_Mela_trst_A-G	-4.644	-2.96
30	Lučane	<i>Prososthenia</i>	<i>schwarzi</i>	L_Pros_schw_A-G	-4.182	-4.506
31	Lučane	<i>Prososthenia</i>	<i>schwarzi</i>	L_Pros_schw_B-G	-5.689	-3.104
32	Lučane	<i>Mytilopsis</i>	<i>jadrovi</i>	L_Myti_jadr_A-G	-4.679	-3.528
33	Lučane	<i>Mytilopsis</i>	<i>jadrovi</i>	L_Myti_jadr_B-G	-4.951	-2.641
34	Lučane	<i>Fossarulus</i>	<i>tricarinatus</i>	L_Foss_tric_A-G	-6.267	-5.047
35	Stuparuša	<i>Melanopsis</i>	<i>bicoronata</i>	S_Mela_bico_A1	-4.736	-4.484
35	Stuparuša	<i>Melanopsis</i>	<i>bicoronata</i>	S_Mela_bico_A2	-6.61	-5.942
35	Stuparuša	<i>Melanopsis</i>	<i>bicoronata</i>	S_Mela_bico_A3	-4.521	-3.775
35	Stuparuša	<i>Melanopsis</i>	<i>bicoronata</i>	S_Mela_bico_A4	-4.44	-5.465
36	Stuparuša	<i>Melanopsis</i>	<i>sinjana</i>	S_Mela_sinj_A1	-4.6	-6.259
36	Stuparuša	<i>Melanopsis</i>	<i>sinjana</i>	S_Mela_sinj_A2	-4.808	-5.564
36	Stuparuša	<i>Melanopsis</i>	<i>sinjana</i>	S_Mela_sinj_A3	-3.958	-4.764
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A1	-4.428	-5.101
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A2	-4.658	-5.349
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A3	-4.577	-5.262
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A4	-3.847	-3.481
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A5	-4.888	-3.812
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A6	-4.71	-4.42
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A7	-4.513	-4.532
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A8	-4.535	-3.997
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A9	-2.666	-2.922
37	Ribarić	<i>Melanopsis</i>	<i>panciciana</i>	F_Mela_panc_A10	-4.4	-3.81
38	Ribarić	<i>Fossarulus</i>	<i>moniliferus</i>	F_Foss_mail_A-G	-4.634	-5.427
39	Ribarić	<i>Fossarulus</i>	<i>moniliferus</i>	F_Foss_mail_B-G	-3.815	-4.105
40	Ribarić	<i>Prososthenia</i>	<i>schwarzi</i>	F_Foss_schw_A-G	-3.708	-2.989
41	Ribarić	<i>Prososthenia</i>	<i>schwarzi</i>	F_Foss_schw_B-G	-4.471	-4.045

Table 1 continued

No.	Locality	Genus	Species	Sample code	d18O	d13C
42	Ribarić	<i>Prososthenia</i>	<i>schwarzi</i>	F_Foss_schw_B/C-G	-4.223	-3.497
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_1	-4.292	-2.946
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_2	-4.678	-2.425
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_3	-5.135	-2.899
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_4	-3.352	-3.004
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_5	-4.775	-2.428
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_6	-5.066	-2.285
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_7	-4.815	-2.179
43	Ribarić	<i>Melanopsis</i>	<i>lyrata</i>	F_Mela_lyra_8	-5.239	-2.468
44	Ribarić	<i>Orygoceras</i>	<i>dentaliforme</i>	F_Oryg_dent_A-G	-3.898	-3.421
45	Ribarić	<i>Orygoceras</i>	<i>dentaliforme</i>	F_Oryg_dent_B-G	-2.99	-2.233
46	Ribarić	<i>Orygoceras</i>	<i>dentaliforme</i>	F_Oryg_dent_C-G	-3.778	-2.82
47	Ribarić	<i>Prososthenia</i>	<i>candidula</i>	F_Lito_cand_A-G	-4.48	-3.412
48	Ribarić	<i>Prososthenia</i>	<i>candidula</i>	F_Lito_cand_B-G	-3.37	-4.133
49	Ribarić	<i>Prososthenia</i>	<i>candidula</i>	F_Lito_cand_C-G	-4.571	-1.932
50	Ribarić	<i>Prososthenia</i>	<i>candidula</i>	F_Lito_cand_D-G	-4.532	-4.907
51	Ribarić	<i>Prososthenia</i>	<i>candidula</i>	F_Lito_cand_E-G	-2.582	-5.052
52	Ribarić	<i>Theodoxus</i>	<i>semidentatus</i>	F_Neri_semid_A1	-4.087	-3.707
52	Ribarić	<i>Theodoxus</i>	<i>semidentatus</i>	F_Neri_semid_A2	-3.611	-2.806
52	Ribarić	<i>Theodoxus</i>	<i>semidentatus</i>	F_Neri_semid_A3	-4.258	-3.327
52	Ribarić	<i>Theodoxus</i>	<i>semidentatus</i>	F_Neri_semid_A4	-4.532	-3.826
52	Ribarić	<i>Theodoxus</i>	<i>semidentatus</i>	F_Neri_semid_A5	-4.312	-3.639
53	Ribarić	<i>Prososthenia</i>	<i>cincta</i>	F_Proc_cinc_A-G-1	-3.438	-3.177
53	Ribarić	<i>Prososthenia</i>	<i>cincta</i>	F_Proc_cinc_A-G-2	-3.362	-3.141
53	Ribarić	<i>Prososthenia</i>	<i>cincta</i>	F_Proc_cinc_A-G-3	-3.51	-3.174
54	Ribarić	<i>Prososthenia</i>	<i>cincta</i>	F_Proc_cinc_B-G-1	-4.035	-4.605
54	Ribarić	<i>Prososthenia</i>	<i>cincta</i>	F_Proc_cinc_B-G-2	-4.155	-4.634
55	Ribarić	<i>Melanopsis</i>	<i>lanzaeana</i>	F_Mela_lanz_A1	-4.276	-4.762
55	Ribarić	<i>Melanopsis</i>	<i>lanzaeana</i>	F_Mela_lanz_A2	-3.403	-4.36
55	Ribarić	<i>Melanopsis</i>	<i>lanzaeana</i>	F_Mela_lanz_A3	-3.549	-4.265
55	Ribarić	<i>Melanopsis</i>	<i>lanzaeana</i>	F_Mela_lanz_A4	-4.369	-4.043
55	Ribarić	<i>Melanopsis</i>	<i>lanzaeana</i>	F_Mela_lanz_A5	-4.709	-4.474

measured: one Dreissenidae species *Mytilopsis jadrovi* (Brusina, 1897) ($n = 2/1-1$), and the Unionidae *Unio rackianus* Brusina, 1874 ($n = 1/11$).

Results

The data set for all taxa is given in Table 1. The $\delta^{18}\text{O}$ values range from -8.48 to -1.56‰ with a mean of -4.6‰ ($\sigma = 1.55$). The $\delta^{13}\text{C}$ range is comparable spanning from -9.03 to -1.93‰ with a mean value

of -4.95‰ ($\sigma = 1.8$). The values are not evenly distributed. Especially, the oxygen values are clearly bimodal with a second peak around -7‰ whilst the carbon values display a less prominent peak between -8 and -9‰ (Fig. 2). In $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross plots, the data arrange roughly along a mixing line from lowest values (e.g. *Orygoceras cornucopiae*, *Prososthenia tournoueri*, *Dianella haueri*, *Emmericia canaliculata*) towards heavy values represented by *Melanopsis plicatula*, *M. visianiana*, *M. zitteli*, *Orygoceras cornucopiae* and *O. dentaliforme* (Fig. 3). The

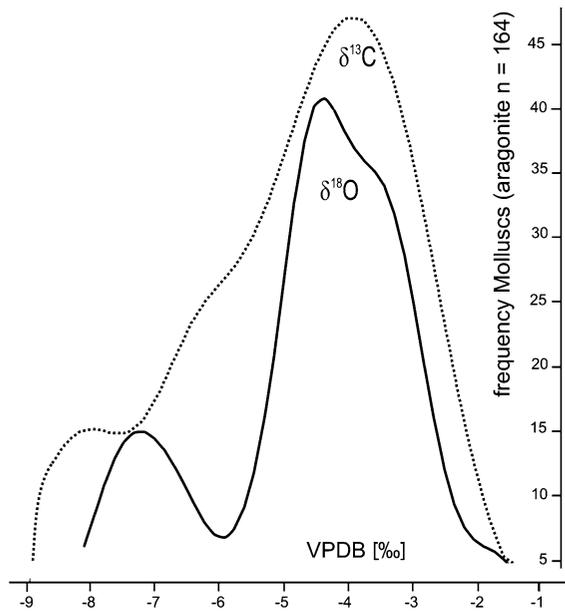


Fig. 2 Frequency diagram of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values from the sampled shells showing a bimodal distribution. This pattern is interpreted to reflect the contribution by a larger group of species from lake settings and a smaller group of species exposed to freshwater influx of springs or rivulets

$\delta^{18}\text{O}/\delta^{13}\text{C}$ covariance of the total data set, however, is poor ($R^2 = 0.14$). This pattern changes if taxa are separated according to localities. Miočić A with 85 data pairs displays a mixing trend and a moderate $\delta^{18}\text{O}/\delta^{13}\text{C}$ covariance ($R^2 = 0.5$). Miočić B ($n = 20$) lacks a reliable correlation ($R^2 = 0.13$) and is characterised by low $\delta^{13}\text{C}$ values. In contrast, the data from Ribarić ($n = 46$) lack any covariance and are concentrated in a bunch of rather heavy values between -2 and -5‰ . The uneven sampling of the various taxa has to be taken into account when interpreting the $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross plots. Multi-sampled taxa such, as the melanopsids, cover a much wider field in the plots than taxa with few measurements.

In the following, each taxonomic group is presented in respect to its ecological requirements and the isotope data (these are given as mean values with standard deviation if at least 3 samples per taxon are available).

Neuritidae

Representatives of the genus *Theodoxus* are usually fresh water dwellers, living in lakes, streams and

estuaries (Bunje, 2005) but may survive even mesohaline conditions (Symanowski & Hildebrandt, 2010). Diatoms and blue green algae films are the preferred food source (Kirkegaard, 2006). Minor amounts of calcite can be present in the outer shell layer of theodoxids (Bandel, 1990). We did not evaluate the contribution by shell calcite and these traces may have altered the values to some degree. *Theodoxus lorkovici* from Miočić displays mean $\delta^{18}\text{O}$ values of -7.56‰ ($\sigma = 0.20$) and -6.68‰ ($\sigma = 0.24$) for $\delta^{13}\text{C}$ whilst *Theodoxus semidentatus* from Ribarić reveals much more positive mean values ($\delta^{18}\text{O} -4.16\text{‰}$, $\sigma = 0.35$; $\delta^{13}\text{C} -3.46\text{‰}$, $\sigma = 0.41$).

Melanopsidae

Melanopsis experienced several outstanding phases of radiation in Neogene lake systems of Europe (Harzhauser & Mandic, 2008). One of these occurred in the DLS where at least 20 endemic taxa are described. Herein, 11 of these species are analysed, giving a good overview about habitat preferences of this group in Lake Sinj. Extant representatives of *Melanopsis* in the circum-Mediterranean area live in freshwater streams and rivers but also in running spring water, lakes and oases (Bilgin, 1973; Bandel et al., 2007). *Melanopsis* tolerates a wide range of temperature, phases of desiccation and slightly brackish waters (Brown, 1994). They are generalists which consume and degrade considerable amounts of leaf litter of trees such as willows or even oleander (Chergui & Pattee, 1991; Heller & Abotbol, 1997).

The studied melanopsids are separated into two groups: *Melanopsis acanthica* from Miočić shows lowest values ($\delta^{18}\text{O} -7.03\text{‰}$, $\sigma = 0.17$; $\delta^{13}\text{C} -5.72\text{‰}$, $\sigma = 0.16$) whilst all other taxa plot within a rather narrow field with heavy values roughly between -5‰ and -2.5‰ for both isotopes: *M. bicoronata* ($\delta^{18}\text{O} -5.08\text{‰}$, $\sigma = 1.03$; $\delta^{13}\text{C} -4.92\text{‰}$, $\sigma = 0.97$), *M. inconstans* ($\delta^{18}\text{O} -3.18\text{‰}$, $\sigma = 1.04$; $\delta^{13}\text{C} -4.62\text{‰}$, $\sigma = 0.29$), *M. lanzaeana* ($\delta^{18}\text{O} -4.06\text{‰}$, $\sigma = 0.56$; $\delta^{13}\text{C} -4.38\text{‰}$, $\sigma = 0.27$), *M. lyrata* ($\delta^{18}\text{O} -4.67\text{‰}$, $\sigma = 0.61$; $\delta^{13}\text{C} -2.58\text{‰}$, $\sigma = 0.32$), *M. panciciana* ($\delta^{18}\text{O} -4.32\text{‰}$, $\sigma = 0.64$; $\delta^{13}\text{C} -4.27\text{‰}$, $\sigma = 0.81$), *M. plicatula* ($\delta^{18}\text{O} -2.71\text{‰}$, $\sigma = 0.72$; $\delta^{13}\text{C} -3.57\text{‰}$, $\sigma = 0.55$), *M. sinjana* ($\delta^{18}\text{O} -4.46\text{‰}$, $\sigma = 0.44$; $\delta^{13}\text{C} -5.53\text{‰}$, $\sigma = 0.75$), *M. trstenjaki* (only one sample: $\delta^{18}\text{O}$

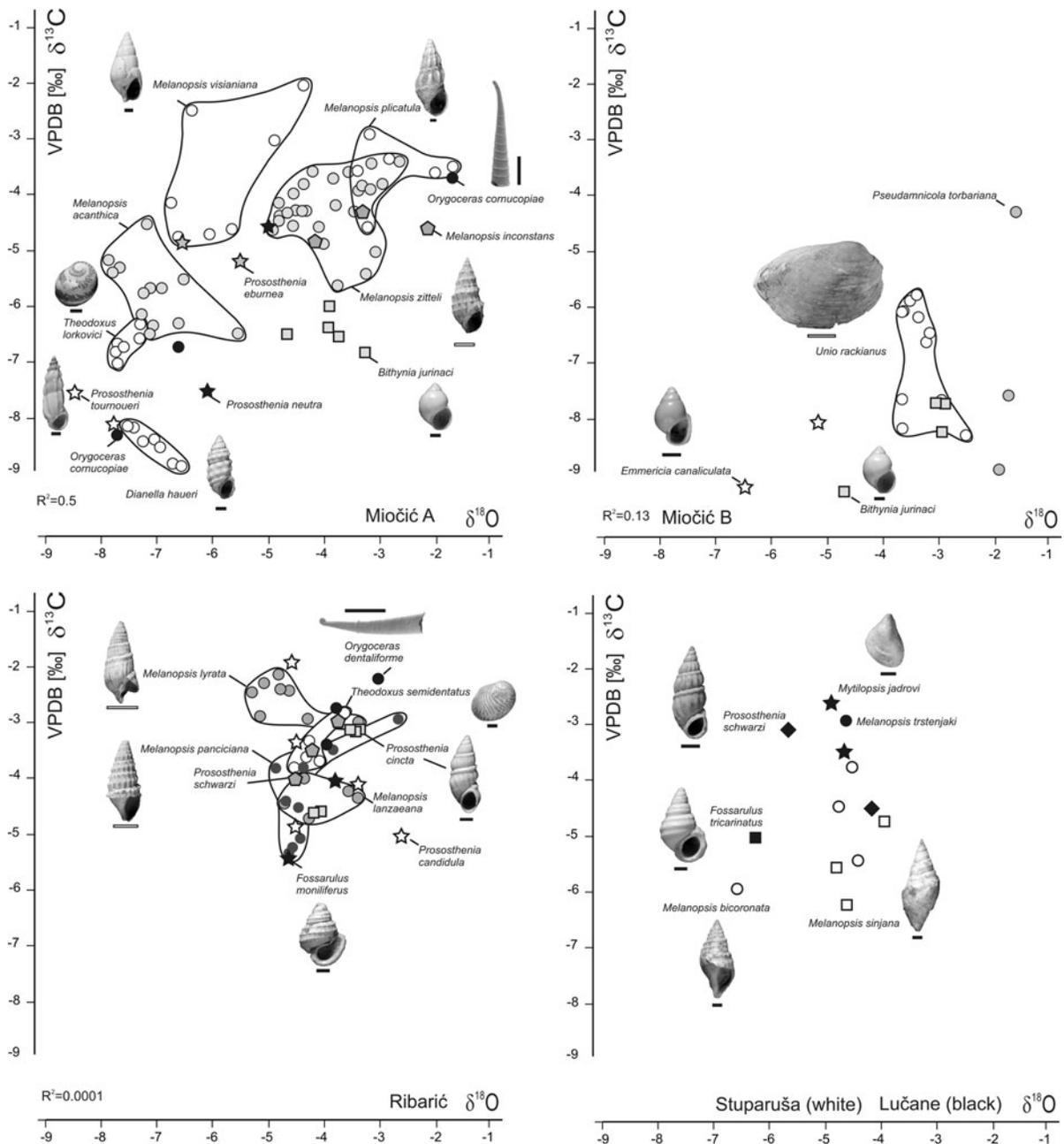


Fig. 3 $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross plots showing the isotope values of most important species separated according to localities and stratigraphic levels. Taxa indicating freshwater influx, such as *Dianella haueri* and *Prososthenia tournoueri* in the data set of

Miočić A are completely missing in Ribarić. Some of the taxa are illustrated to show the morphological diversity of this endemic fauna (black scale bars = 1 mm, white scale bars = 5 mm)

-4.64‰ ; $\delta^{13}\text{C} -2.96\text{‰}$), *M. visianiana* ($\delta^{18}\text{O} -4.82\text{‰}$, $\sigma = 0.75$; $\delta^{13}\text{C} -3.64\text{‰}$, $\sigma = 1.15$) and *M. zitteli* ($\delta^{18}\text{O} -3.91\text{‰}$, $\sigma = 0.67$; $\delta^{13}\text{C} -3.85\text{‰}$,

$\sigma = 0.66$). This grouping suggests a comparable habitat and food source for most of the melanopsids and an environment with depleted isotope values for

M. acanthica. This group comprises species from Lučane, Ribarić and Miočić and does not separate into localities.

Bithyniidae

Extant species of *Bithynia* are freshwater dwellers, living in slowly running rivulets, ponds and lakes in depth up to 5 m and often indicate calcium-rich waters (Jokinen, 1992). Some species, however, may even estuaries with salinities of up to 4 psu (Reinhardt et al., 2003). Thus, the occurrence of *Bithynia* in the fossil record should not be used as fool-proof indicator for pure freshwater habitats. The animals attain an age of up to 3 years and are able to switch from grazing to filter feeding utilising algae and detritus (Jokinen, 1992; Brendelberger & Jürgens, 1993). Recently, Anadón et al. (2010) proved that *Bithynia* precipitates its shell in isotopic equilibrium with the ambient water and excellently reflects changes in water temperature.

The analysed shells of *Bithynia jurinaci* have rather heavy oxygen values ($\delta^{18}\text{O}$ -3.66% , $\sigma = 0.70$) but strongly negative carbon values ($\delta^{13}\text{C}$ -7.27% , $\sigma = 1.06$). A similar relation, with moderately negative oxygen values but strongly negative carbon values has been documented from lake dwelling Holocene *B. tentaculata* from Ireland (Conroy, 2003) and from *B. phialensis* in a modern estuary in Israel (Reinhardt et al., 2003). This consistent pattern might point to the contribution of light dietary carbon.

Hydrobiidae

Prososthenia is an extinct hydrobiid genus which appeared during the late Early Miocene and vanished during the Early Pleistocene. The occurrences suggest that it was a pure freshwater dweller living in lakes and ponds (Esu & Girotti, 2001). Similarly, *Fossarulus* is an extinct genus which vanished during the Pliocene and seems to have preferred similar habitats like *Prososthenia*. The extant species of *Emmericia* live in freshwater lakes and springs along the eastern Adriatic coast and occur even in caves and subterranean rivulets (Schütt, 2000). This group, too, displays a bimodal distribution. Most taxa plot in the moderate negative field of the $\delta^{18}\text{O}/\delta^{13}\text{C}$ graph: *P. candidula* ($\delta^{18}\text{O}$ -3.91% , $\sigma = 0.90$; $\delta^{13}\text{C}$

-3.89% , $\sigma = 1.28$), *P. cincta* ($\delta^{18}\text{O}$ -3.7% , $\sigma = 0.37$; $\delta^{13}\text{C}$ -3.75% , $\sigma = 0.80$), *P. schwarzi* ($\delta^{18}\text{O}$ -4.94% ; $\delta^{13}\text{C}$ -3.81%), *P. dalmatica* ($\delta^{18}\text{O}$ -3.29% ; $\delta^{13}\text{C}$ -4.95%), *F. moniliferus* ($\delta^{18}\text{O}$ -4.23% ; $\delta^{13}\text{C}$ -4.77%). The rest forms a gradual transition into strongly negative values: *P. neutra* ($\delta^{18}\text{O}$ -5.52% ; $\delta^{13}\text{C}$ -6.10%), *E. canaliculata* ($\delta^{18}\text{O}$ -5.78% ; $\delta^{13}\text{C}$ -8.65%), *F. tricarinatus* ($\delta^{18}\text{O}$ -6.27% ; $\delta^{13}\text{C}$ -5.05%), *P. eburnea* ($\delta^{18}\text{O}$ -6.01% ; $\delta^{13}\text{C}$ -5.04%), *P. tournoueri* ($\delta^{18}\text{O}$ -8.12% ; $\delta^{13}\text{C}$ -7.90%).

Extant *Pseudamnicola* are grazers and deposit feeders (Gofas, 2010), occur in slowly running spring-fed-freshwater bodies and channels (Djamali et al., 2006; Gloer & Zettler, 2007) but also in slightly brackish estuaries and even in saline spring streams (Moreno et al., 2010). The oxygen values in *Pseudoamnicola torbariana*, however, do not correspond to very negative values as expected for spring-water-dwellers, but are outstanding high, ranging around -1.6% . In contrast, the $\delta^{13}\text{C}$ values range from very negative values at -8.98% to moderate negative values of -4.27% .

The generic placement of *Dianella haueri* within *Dianella* is only preliminary and will need further studies. Extant *Dianella* inhabit SE European fresh water habitats (Szarowska et al., 2005). In our data set, *Dianella haueri* reveals the most negative mean values with mean $\delta^{18}\text{O}$ values of -7.09% ($\sigma = 0.33$) and mean $\delta^{13}\text{C}$ values of -8.50% , $\sigma = 0.31$). The range of isotopic signatures of the various hydrobiids, thus, indicates a specialisation to very different palaeoenvironments. The rather narrow ranges of the single taxa might expand if more samples would be measured (as for the multi-sampled melanopsids) but the general pattern seems to be robust.

Planorbidae

The extinct *Orygoceras* is one of the most conspicuous gastropods in the fauna of the Dinarid Lakes. It is characterised by a decoiled shell with a long and straight last whorl. Its relation to planorbids was inferred based on its striate protoconch sculpture (Harzhauser et al., 2002). This genus is known from the Dinarid Lake System and Lake Pannon, suggesting a refuge for the genus for more than 5 My. Later, it might have survived even up to the Messinian when it is reported from the Velona Basin in Italy (Ghetti

et al., 2002). Nothing is known about its ecology and the reason for its success in these two very different lake systems is unclear. Modern planorbids settle a wide range of freshwater habitats from lakes to slowly running rivers and floodplains. Their diet consists of bacteria, algae, organic debris and leaf litter (Calow, 1975; Falkner et al., 2001). Two species have been analysed herein; each measurement is based on the total shell, the resulting values represent average values across the life-span of each animal. *Orygoceras dentaliforme* values plot in a narrow area with a mean $\delta^{18}\text{O}$ values of -3.56‰ ($\sigma = 0.49$) and mean $\delta^{13}\text{C}$ values of -2.83‰ ($\sigma = 0.59$). In contrast, the three specimens of *Orygoceras cornucopiae* encompass a very wide $\delta^{18}\text{O}$ range from -7.76 and -6.63‰ up to -1.67‰ and from -8.37 and -6.78‰ up to -3.72‰ in $\delta^{13}\text{C}$. The latter species spans the entire mixing line. This pattern might either point to a wide range of habitats settled by this species or to a change of habitat during ontogeny.

Bivalvia

Unio species inhabit clean freshwater ecosystems such as oxbow lakes, creeks or rivers with sandy to muddy bottoms (Ricken et al., 2003). They feed on organic detritus which is filtered from the ambient water. Very similar habitat requirements and feeding strategy is suggested for the small dreissenid *Mytilopsis jadrovi*, which might have lived attached to hard grounds similar to modern *Dreissena*. All sampled bivalve shells have rather high oxygen values (*Unio rackianus*: $\delta^{18}\text{O}$ mean -3.33‰ , $\sigma = 0.36$; *Mytilopsis jadrovi* ($\delta^{18}\text{O}$ -4.68 to -5.00‰) but differ in the carbon values. These are quite negative in the unionids ($\delta^{13}\text{C}$ mean -6.87‰ , $\sigma = 0.95$) but distinctly less negative for the dreissenid ($\delta^{13}\text{C}$ -3.53 to -2.64‰).

Discussion

Stable isotope composition of the palaeolakes

The water chemistry of lakes was strongly influenced by the karstic environment which favoured the development of an alkaline hard-water system (Mandic et al., 2009). Pollen data document a succession of rather warm and dry climate phases alternating with longer phases of warm and humid

conditions (Jiménez-Moreno et al., 2008). The dry phases are indicated by an increase of xeric plants and a shift in sedimentology from fossil-poor limestones into coal-bearing carbonate rocks and coal seams. During these phases, the lake chemistry stabilised at a high alkalinity level and mollusc radiations were initiated (Mandic et al., 2009). The $\delta^{18}\text{O}_{\text{water}}$ of the DLS during these periods can be expected to have been enriched in heavy isotopes due to evaporation and a low lake level. Modern lakes of the Balkan Peninsula, too, display high $\delta^{18}\text{O}_{\text{water}}$ values due to evaporative effects. Lake Ohrid, an ancient lake at the boundary between Macedonia and Albania, displays $\delta^{18}\text{O}_{\text{water}}$ values ranging between -2.5 and -4.5‰ whilst the adjacent smaller Lake Prespa ranges between c. -2 and -1‰ (Matzinger et al., 2006; Leng et al., 2010). The much shallower Lake Dojran at the boundary between Greece and Macedonia has a $\delta^{18}\text{O}_{\text{water}}$ of $+2\text{‰}$ (Griffiths et al., 2002). Other hydrologically isolated shallow water lakes in Central Europe such as Lake Balaton in Hungary and Lake Neusiedl in Austria have values between -1 and -3‰ (Darling, 2004).

No direct evidence for coeval early Middle Miocene rivers is available in the study area. Due to the limestone catchment area no siliciclastic load is transported and the best studied Lučane section did not bear sedimentologic evidence for riverine input (Mandic et al., 2009). Despite the absence of a major river, we interpret the strongly negative oxygen values as expression of freshwater influx by springs or rivulets, lowering the elevated isotope level of the lake water. Modern rivers in the area have isotopically rather heavy $\delta^{18}\text{O}$ values of c. -8‰ and $\delta^{13}\text{C}_{\text{DIC}}$ values of c. -12 to -13‰ (Lojen et al., 2004). These data fit excellently to the observed freshwater end-member data in the mollusc aragonite. Even usually isotopically light groundwater may reach extremely high $\delta^{13}\text{C}$ values in karstic areas (Leng & Marshall, 2004). Therefore, the freshwater end-member in the data set may also be influenced by springs.

Comparison with modern molluscs from Balkan lakes is hampered by the very spotty stable isotope data. *Anodonta* shells from Lake Dojran display $\delta^{18}\text{O}$ values of c. -1 to $+2\text{‰}$ and $\delta^{13}\text{C}$ values of c. -8 to -5‰ (Griffiths et al., 2002).

The disjunct distribution of syngeneric species in the $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross plots indicates sympatric habitat

segregation. E.g. *Melanopsis acanthica* seems to have preferred areas with freshwater influx whilst *Melanopsis zitteli*, *M. inconstans* and *M. plicatula*, settled lake waters with elevated oxygen isotope signatures such as evaporated coastal waters (Fig. 3). A comparable specialisation to freshwater influenced habitats is postulated for *Prososthenia tournoueri* and *Theodoxus lorkovici* whilst *Prososthenia cincta* and *Theodoxus semidentatus* represent the “heavy” lake end-member counterparts. This habitat separation between syngeneric species might be a main factor controlling the radiative success of the endemic mollusc faunas in the Dinaride Lakes System. This hypothesis will have to be tested by detailed analyses of palaeoassemblages from the sections. This, however, is beyond the scope of this study and is hampered by the fact that some of the localities are historical and now inaccessible.

Temperature, seasons and the palaeobotanical feedback

DLS $\delta^{18}\text{O}_{\text{water}}$ can also be calculated based on the $\delta^{18}\text{O}_{\text{aragonite}}$ of *Unio rackianus* as unionids-growth ceases below 10–12°C (Dettman, 1999). Following the equation of Grossman & Ku (1986), the relation between temperature (T), $\delta^{18}\text{O}_{\text{water}}$ and $\delta^{18}\text{O}_{\text{aragonite}}$ is: $T^{\circ}\text{C} = 20.6 - 4.34 (\delta^{18}\text{O}_{\text{water}} - \delta^{18}\text{O}_{\text{aragonite}})$. This assumption would point to a $\delta^{18}\text{O}_{\text{water}}$ of c. -4.5 to -5‰ to meet the required growth temperatures of the unionid.

Calculating these realistic boundaries for the $\delta^{18}\text{O}_{\text{water}}$ values, the data set from Ribarić would reflect a total temperature range of 11.5°C within a range from c. 10–12.3°C up to 21.6–23.8°C with a mean value of 16.9–19.1°C. Due to the influx of the freshwater end-member taxa, Miočić A displays a much wider range of 29°C starting from c. 6.1–8.3°C up to 35.7–37.9°C with a mean of 21.0–23.2°C. Distinctly cooler conditions are indicated by the stratigraphically younger samples from Miočić B (mean: 13.4–15.3°C; ranging from 5.6–7.8°C to 26.8–29.0°C).

Due to the many unknown variables, these estimations are clearly only approximations and have to be treated with caution. A more reliable proxy is the within-shell-range, which reflects the range of temperatures to which the individual was exposed to during growth (Fig. 4). In both sample sets from

Miočić A and Ribarić the within-shell-ranges suggest a seasonal variation of c. 10°C. This range is represented in *Melanopsis zitteli* (10°C), *M. acanthica* (10°C) and *M. panciana* (9.7°C). *Melanopsis visianiana* (8.6°C), *M. lyrata* (8.2°C) and *Prososthenia candidula* (8.7°C) are close to that value. This group is opposed by taxa with very low variation in $\delta^{18}\text{O}$, suggesting quite stable water temperatures throughout ontogeny. These are *Prososthenia cincta* (3.5°C) and *Dianella haueri* (4°C) whereas the data on *Theodoxus lorkovici* (1.8°C) and *Theodoxus semidentatus* (4°C) may be biased by the mixed shell-mineralogy. Low temperature variation is also documented for *Unio rackianus* (5.5°C) and *Melanopsis lanzaeana* (5.7°C). Most of these taxa fall also in the freshwater end-member group and support the interpretation of a freshwater fed environment in which seasonal temperature shifts are damped. These taxa have also the lowest ranges in $\delta^{13}\text{C}$ which fit to the assumption that they have been supplied with a rather constant DIC pool.

A clear and predictable relation exists between lake surface water temperature and mean annual air temperature (McCombie, 1959; Grafenstein et al., 1996; Livingstone & Dokulil, 2001; Dokulil et al., 2006; Sharma et al., 2008). Generally, a slightly positive offset of water temperature from the air temperature occurs. Therefore, the lake water temperature and its seasonal range deduced from shell carbonate can be tested with climate estimates deduced from palaeobotanical data. In total, 39 different plant taxa were listed in literature from the Lučane section based on pollen (Jiménez-Moreno et al., 2008) and leaves (Kerner, 1905a, b). All together were analysed by the Coexistence Approach of Mosbrugger & Utescher (1997), a method based on the relationship between the fossil taxa and their most appropriate nearest living relative. By determining the closest recent representative of each taxon, modern climatic data can be used to give an idea about the past climate. All the climatic information is given as a climatic interval, in which all the nearest living relatives of plants would be able to survive (Coexistence Interval). This method reveals several palaeoclimatic data such as the mean annual temperature (MAT), the mean temperature of the coldest and warmest months (CMT, WMT), the mean annual precipitation (MAP), the mean precipitation of the wettest and driest months (MPwet, MPdry) and the mean precipitation of the

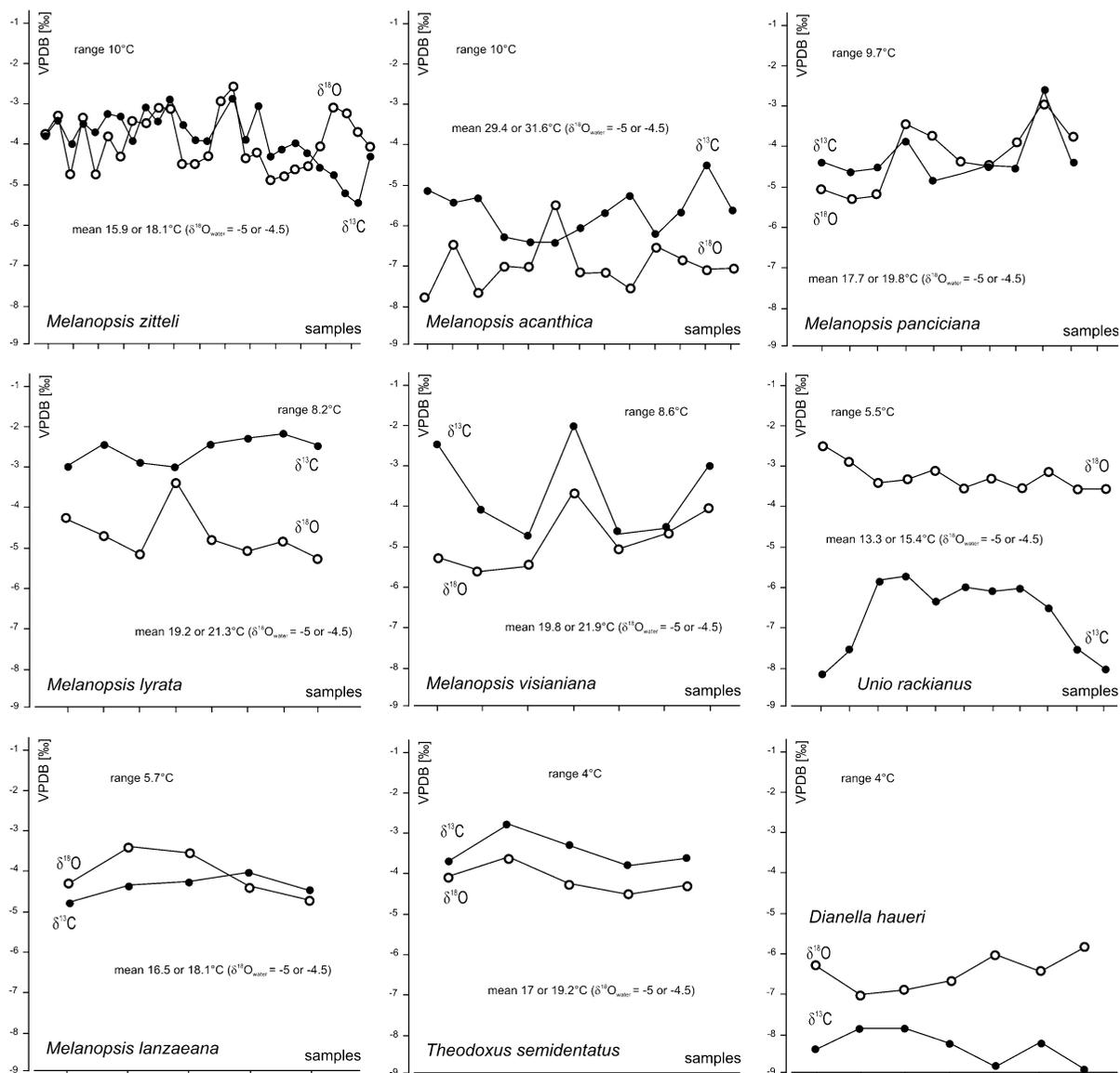


Fig. 4 Sclerochronological analysis of several typical DLS species. The ranges are suggested to reflect seasonal shifts in temperature and DIC pool

warmest month (MPwarm). This method indicates following climatic conditions: temperature: MAT 16.5°C (ranging from 15.6 to 17.4°C), CMT 7.3°C (5.0–9.6°C), WMT 26°C (25.8–26.1°C). Precipitation data suggest a MAP interval of 974 to 1,150 mm with a mean of 1,062 mm with a MPwet of 175 mm (125–225 mm), MPdry 33 mm (11–55 mm) and a MPwarm of 115 mm (89–141 mm). The plants limiting the Coexistence Intervals reflect the climatic description by Jiménez-Moreno et al. (2008) of a

warm, subtropical climate with some xeric phases very well. Important index taxa are *Engelhardia* and *Distylium*, which are both restricted today to the warm climate of south and south-east Asia. Because of its mainly tropical distribution, *Diospyros* is another indicator for high temperature. Several tropical and subtropical taxa such as *Platycarya*, *Ficus* and *Distylium* give a strong signal for a general humid climate, fitting to the Miocene Climate Optimum of the early Middle Miocene. Nevertheless, taxa, which are

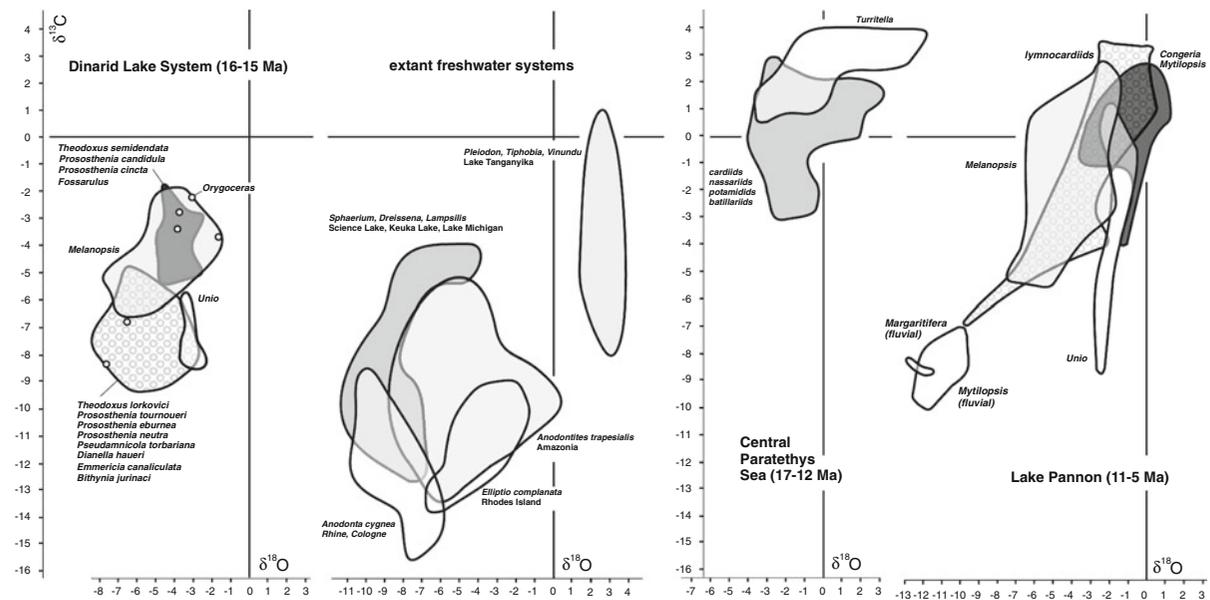


Fig. 5 Comparison of the isotope signatures of various marine, brackish and freshwater systems in $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross plots. No influence by coeval marine waters of the Central Paratethys are detectable. Data sources: DLS: this study; extant freshwater systems: Fastovsky et al. (1993), Dettman (1999), Dettman et al.

(2005), Wurster & Patterson (2001), Ricken et al. (2003), Vonnhof et al. (2003), Kandoorp et al. (2003, 2005); Paratethys Sea: Latal et al. (2004, 2005, 2006), Harzhauser et al. (2007a, b); Lake Pannon: Geary et al. (2002), Mátyás et al. (1996), Harzhauser et al. (2007a, b)

resistant to dry phases, appear as well. These have the nearest living relatives in central south-USA (e.g. *Juglans rupestris* and *Bumelia lanuginosa*) or in the Mediterranean area (e.g. *Quercus ilex-coccifera*) suggest dryer conditions either due to seasonality or due to xeric habitats close by.

These data are in agreement with interpretation of the $\delta^{18}\text{O}$ values. A mean annual air temperature around $\sim 16\text{--}17^\circ\text{C}$ fits well to slightly warmer lake surface water temperatures of roughly $\sim 19\text{--}21^\circ\text{C}$. The broad temperature range of $\sim 19^\circ\text{C}$ between the coldest month to the warmth month is clearly damped in the lake. Moreover, the spotty measurements of the shells, which were not conducted as high resolution sclerochronologic analysis, will certainly not represent the entire seasonal range.

Carbon signatures

The $\delta^{13}\text{C}_{\text{shell}}$ values of the total data set have a peak around -4.5 to -3‰ (Fig. 2). These are distinctly more negative than the bulk sample data on authigenic carbonate which peak around -2 to -1‰ (unpublished own data). $\delta^{13}\text{C}_{\text{shell}}$ of aquatic gill-breathing molluscs is considered to be mainly

influenced by dissolved inorganic carbon (DIC) of ambient water (McConnaughey & Gillikin, 2008). Nevertheless, influence by dietary carbon and metabolic processes are suggested in many studies to contribute to the animals' carbon budget as well (Dettman, 1999; Geist et al., 2005; Gajurel et al., 2006). This contribution may explain the generally lower values of mollusc carbonate compared to the bulk sample values of authigenic carbonate, which might be closer to equilibrium with the ambient water. Therefore, the feeding strategy might be reflected in the data as well. The measured molluscs represent various ecological guilds and represent filter feeders, grazers, detritivores and leaf litter consumers and mixed feeding types. Grazing on algae implies the uptake of carbon signatures of phototrophic biofilms with a range from -36 to -19‰ in freshwater systems (Staal et al., 2007). These values are strongly overlapping with C3 plants, on which leaf litter consumers depend and which have a range from -20 to -32‰ (Leng & Marshall, 2004). Freshwater phytoplankton, which might contribute to the carbon budget of the filter feeders has a similar range from -42 to -26‰ (Leng & Marshall, 2004; Geist et al., 2005). In our data set, no

correlation of any of the supposed feeding strategies with a certain $\delta^{13}\text{C}$ value can be stated although a wide range from -9.30 to -1.93‰ is represented. Filter feeding might be expected to cause slightly more negative values as represented in *Unio rackianus*. *Mytilopsis jadrovi*, however, displays very high $\delta^{13}\text{C}$ values. Especially, the bimodal distribution of carbon values in the hydrobiids, which represent comparable feeding strategies within the group, suggests that the $\delta^{13}\text{C}$ value of the shell is largely driven by the DIC pool of the ambient water (at least within the resolution of our data).

The Dinaride Lake System and the sea

Several striking examples of parallel evolution in melanopsids, planorbids and dreissenids are documented from the Dinaride Lake System and the much younger, marine-derived Lake Pannon (Harzhauser & Mandic, 2008). Both lake systems are slightly alkaline (Harzhauser et al., 2007a, b; Mandic et al., 2009). Therefore, it is tempting to propose similar water chemistry as an important factor influencing the endemic evolution in these lakes. Marine influx, causing brackish conditions, could have penetrated the DLS from the proto-Mediterranean Sea in the southwest or from the Central Paratethys Sea in the northeast (Rögl, 1998). Popov et al. (2004) even indicate paralic facies on their palaeogeographic maps. Comparable, marine ingressions are at least documented for the Pleistocene (Jurišić-Polšak et al., 1992).

Our data set, however, questions this interpretation. On the one hand, the composition of the mollusc fauna points to freshwater habitats. Typical Early and Middle Miocene brackish water taxa, such as batiilliid and potamidid gastropods, are completely missing. On the other hand, the new stable isotope data differ distinctly from Miocene marine and brackish isotope signatures of adjacent systems. A large amount of stable isotope data on mollusc aragonite from the Central Paratethys has been published by Latal et al. (2004, 2005, 2006) and Harzhauser et al. (2007b). Data on Lake Pannon were provided by Geary et al. (2002), Mátyás et al. (1996) and Harzhauser et al. (2007a, b). In Fig. 5, these data are outlined in $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross-plots to reveal the overall isotope regime in each palaeogeographic entity. Typical marine values characterise the Central

Paratethys data set. The heritage of these signatures is evident in the Lake Pannon data set, which largely overlaps with its precursor, but clearly shows a tendency towards lighter values as typical in brackish water environments. The isotope signature of the DLS, however, is clearly distinct from these and lacks the “marine tail” of positive carbon and oxygen values. Among published mollusc aragonite records from extant freshwater systems a much better fit is given with the isotope signatures from Amazonian wetlands (Kandoorp et al., 2003, 2005; Vonhof et al., 2003) and several lakes of North America (Dettman, 1999; Wurster & Patterson, 2001). Stable isotope patterns in mollusc aragonite from strongly evaporated tropical lakes, such as Lake Tanganyika, differ in their even more elevated oxygen values (Dettman et al., 2005). The data have a good fit with the scattered data on molluscs from extant Balkan lakes, such as Lake Dorjan, which is a pure freshwater lake (Griffiths et al., 2002). Similarly, there is a good overlap with data on Quaternary authigenic calcite from the freshwater lakes Ohrid and Prespa (Leng et al., 2010).

The DLS is interpreted as a closed freshwater system without marine influence but with enough contribution of freshwater to keep the oxygen values close to -5‰ . The overall rather high values in both stable isotopes result from a combination of evaporation effects and the influx of already isotopically heavy freshwater from the karstic catchment area.

Conclusions

The lakes of the DLS harboured a diverse endemic mollusc fauna. They represent slightly alkaline freshwater lakes that developed under subtropical conditions (Mandic et al., 2009). Pulses of radiation in molluscs correspond largely to more arid phases when coal seams formed and the lake level was lowered (Jiménez-Moreno et al., 2008; Mandic et al., 2009). Consequently, the lake water was enriched in heavy isotopes due to evaporation. Moreover, the input of isotopically heavy water from the karstic limestone catchment area amplified the tendency towards $\delta^{18}\text{O}_{\text{water}}$ values of about -4.5 to -5‰ . These values are also in good agreement with minimum temperature calculations based on $\delta^{18}\text{O}_{\text{shell}}$ values in unionid bivalves. Palaeowater temperature

estimates are difficult due to the amount of poorly defined variables. Nevertheless, a mean surface water temperature of c. 19–21°C and a seasonal range of c. 10–11°C are suggested by the data for the DLS during the Miocene Climatic Optimum. This estimate is supported by the palaeobotanical data, which indicate slightly cooler mean annual air temperatures of c. 16–17°C.

A slight decrease of mean water temperatures of c. 14–15°C is indicated by the stratigraphically youngest samples from Miočić B. The coeval samples from the Drniš Basin (Miočić A) and from the Sinj Basin (Lučane, Stuparuša, Ribarić) have very similar isotope signatures. Therefore, a tight hydrological connection between these basins within the DLS is proposed. Despite the elevated $\delta^{18}\text{O}$ level, the influence by marine waters from the close by proto-Mediterranean Sea in the southwest or the Paratethys Sea in the NE is rejected. A comparison with isotope values from the late Miocene Lake Pannon, with clearly brackish water conditions, shows that the $\delta^{18}\text{O}_{\text{shell}}$ values of the DLS taxa are much closer to extant freshwater systems than to the marine-derived Lake Pannon waters. Similarities in the water chemistry can therefore be discarded as trigger for morphological parallel evolution in both lakes.

The fauna comprises mainly lake dwelling taxa which are indicated by elevated isotope values and large seasonal ranges. A smaller portion is represented by taxa with depleted isotope values typical for freshwater end-member carbonates. These may have preferred environments in the sphere of influence of spring water and/or rivulets. Typically, these taxa show small seasonal temperature ranges and little variation in carbon due to the more stable habitat. Species of the same genus, e.g. among *Melanopsis* and *Prososthenia*, plot in quite distinct and separate fields in the $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross plots. This points to a habitat segregation of congeneric taxa within the various lake environments and suggests even utilisation of different food sources. This habitat segregation may have played a major role for the sympatric evolution of the DLS mollusc fauna. This hypothesis is supported by biodiversity analyses in modern lake systems which suggest a strong influence by vertical and horizontal gradients causing segregation in the spatial distribution of populations, supporting parapatric speciation (Albrecht et al., 2006, 2008; Hauffe et al., 2010; Trajanovski et al.,

2010). A weak point in this hypothesis, however, is that up to now only isotope data can be used for the interpretation whereas detailed analysis of palaeoassemblages from the sections are missing.

Within the locality and stratigraphic level, different mollusc species clearly exhibit different isotope signatures. These are caused by habitat segregation and local variations in the lake environment. Neither $\delta^{18}\text{O}$ nor $\delta^{13}\text{C}$ pools are homogenous in the varied environments of lake shores. This ‘taxonomic’ factor has to be kept in mind in isotope studies dealing with long-term changes in lake systems, based on a mixing of different taxonomic groups and a variety of species.

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