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Authors: Lukeneder, Susanne, Zuschin, Martin, Harzhauser, Mathias, and Mandic, Oleg

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Spatiotemporal signals and palaeoenvironments of endemic molluscan assemblages in the marine system of the Sarmatian Paratethys

SUSANNE LUKENEDER, MARTIN ZUSCHIN, MATHIAS HARZHAUSER, and OLEG MANDIC

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The present study is the first quantitative comparison of Sarmatian mollusc assemblages from the Central and Eastern Paratethys seas. The assemblages (47,840 shells, 32 samples, 84 species) derive from eight Middle and Upper Miocene localities covering an interval from 12.7–11.0 Ma, when a highly endemic mollusc fauna flourished in the entire Paratethys. Cluster analysis of samples yields two major clusters: one composed of late Sarmatian (Bessarabian) collections and the other composed of early Sarmatian (Volhynian) collections. The Volhynian cluster includes two subclusters: the first reflects a strong stratigraphic signal because it combines samples from the *Mohrensternia* Zone of the Vienna Basin and the western Ukraine. The second combines samples from the Upper *Ervilia* Zone of the Vienna Basin with samples from the *Mohrensternia* Zone of the Vienna Basin and Romania. Cluster analysis of species indicates that the sample clusters represent different palaeoenvironments with distinct molluscan assemblages: The Volhynian well-agitated shore is characterized by the *Granulolabium–Venerupis–Ervilia* biofacies, the Volhynian muddy foreshore by the *Granulolabium–Mohrensternia–Ervilia* biofacies, and the Bessarabian shallow to medium deep sublittoral by the *Hydrobia–Venerupis–Pseudamnicola* biofacies. Although not all biozones and regions of the Sarmatian Sea are covered, we suggest that these biofacies cover a wide range of possible assemblage compositions of Sarmatian nearshore and shallow-water assemblages.

Key words: Bivalvia, Gastropoda, endemism, Volhynian, Bessarabian, Miocene, Paratethys Sea.

Susanne Lukeneder [Susanne.Lukeneder@nhm-wien.ac.at], and Martin Zuschin [martin.zuschin@univie.ac.at], Department of Palaeontology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria;
Mathias Harzhauser [mathias.harzhauser@nhm-wien.ac.at] and Oleg Mandic [oleg.mandic@nhm-wien.ac.at], Geological-Palaeontological Department, Natural History Museum Vienna, Burgring 7, A-1010 Vienna, Austria.

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Introduction

During the Middle Miocene, at 12.7 Ma, the Paratethys Sea became almost completely separated from the Mediterranean basins (Rögl and Steininger 1984; Rögl 1998; Popov et al. 2004). The semi-enclosed sea extended from eastern Austria to the Caucasus (Fig. 1) and was populated by an increasingly endemic fauna with comparatively low number of species but high morphological variety (Rögl and Steininger 1984; Rögl 1998, 1999; Harzhauser and Kowalke 2002; Harzhauser and Piller 2004a, b). The so-called Paratethyan mollusc faunas are characterised by their morphological exuberance, high diversity and endemism (Wesselingh et al. 2008). Cox and Moore (1993) as well as Hills et al. (1996) defined endemism as the restriction of a taxon or a community to a particular geographical area. Evolutionary processes, like speciation, extinction and community turnover can be inferred by patterns of endemism (Simison 2006). Increased endemism as well as reduced diversity are the results of ecological isolation (Diamond 1972; Wilcox 1978; Brown and Gibson 1983; Case and Cody 1987; Case et al. 1992; Myers and Giller 1988; Simison 2006). During the Volhynian, the Central and Eastern Paratethys were united and offer a strikingly similar faunistic inventory (Kolesnikov 1935; Papp 1974b; Harzhauser and Piller 2004b).

The mollusc fauna of the Vienna Basin and the Pannonian Basin System has been intensively studied, but quantitative data allowing further correlation with the Eastern Paratethys are sparse. Moreover molluscs have mostly been used for stratigraphic zonation (Fig. 2; Papp 1954; Harzhauser and Piller 2004b), but palaeocommunity comparisons are lacking. The present study was designed to provide the first quantitative comparison of Sarmatian, respectively Volhynian and Bessarabian, mollusc assemblages from the Eastern and Central Paratethys, to test the role of spatial and temporal factors and to decipher their palaeoenvironments. For this

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Table 1. Number of samples per time interval and region.

	Vienna Basin	Romania	Western Ukraine	Crimea
Bessarabian	–	–	–	12
Sarmatimactra vitaliana Zone	–	–	–	–
Upper *Ervilia* Zone	11	–	–	–
Lower *Ervilia* Zone	–	–	–	–
Mohrensternia Zone	4	2	3	–

Table 2. Stratigraphic, environmental, and sedimentological assignment for each sample.

Sample	Environment	Stratigraphy	Sedimentologic assignment (facies)
Zavjetnoje 1	shallow to moderately deep sublittoral	Bessarabian	silt and sand with diatomitic marl, crossbedded oolithic sand, molluscan shell beds
Zavjetnoje 3			
Zavjetnoje 4			
Zavjetnoje 6			
Zavjetnoje 7			
Zavjetnoje 8			
Zavjetnoje 9			
Zavjetnoje 10			
Jurkino 1			
Jurkino 2a			
Jurkino 2b			
Jurkino 2c			
Soceni Poltioană 3	well agitated shore with high freshwater influx	*Mohrensternia* Zone	tempestitic layers
Soceni Poltioană 7			
Zhabiak 6/9	muddy foreshore phytogen associated	*Mohrensternia* Zone	sandy tempestitic layers, well agitated sand bottom
Zhabiak 6/11			
Zhabiak 6/12			
Siebenhirten 1	muddy foreshore	*Mohrensternia* Zone	sandy channel structure, intertidal mud flat channel
Siebenhirten 2			
Siebenhirten 3	ooid shoal		coastal mud flat
Siebenhirten 4	muddy foreshore/phytogen associated		silty deposits containing mostly rissoid gastropods (*Mohrensternia*), and shells of *Abra reflexa*
Nexing 1	ooid shoal	Upper *Ervilia* Zone	cross bedded flood tidal deposits containing transported shells
Nexing 2			
Nexing 3			
Hauskirchen 1	ooid shoal	Upper *Ervilia* Zone	wavy oolitic sandlayers
Hauskirchen 2			
Hauskirchen 3			
Hauskirchen 4			
Kettlasbrunn 1	well agitated ooid shoal	Upper *Ervilia* Zone	cross bedded sandlayers
Kettlasbrunn 2			
Kettlasbrunn 3			
Kettlasbrunn 4			

purpose, 47,840 shells from 32 samples with 84 species from 8 localities were quantitatively compared (Tables 1, 2). The abundant species are listed (Table 3) and figured (Figs. 3, 4).

Other abbreviation.—NAFB, North Alpine Foreland Basin.

Geologic and stratigraphic setting

The term Sarmatian is based on endemic mollusc faunas and is therefore restricted to the Paratethys (Papp 1974a). The Sarmatian of the Central Paratethys spans an interval from 12.7 to 11.6 Ma and represents a marine sea with endemic fauna. Due to geodynamic processes, this development terminates with the onset of the Late Miocene, when Lake Pannon formed within the Pannonian Basin System. In the Eastern Paratethys, no such interruption took place, and marine conditions lasted far into the Late Miocene (Harzhauser and Piller 2004b). Due to these palaeogeographical differences in the durations of marine conditions the term "Sarmatian sensu strico" is used for the Central Paratethys. The rapid endemic evolution and the switch from siliciclastic to carbonate sedimentation allowed a further subdivision into eco-biozones: The *Mohrensternia* Zone, the Lower and Upper *Ervilia* zones, and the *Sarmatimactra vitaliana* Zone. These eco-biozones are an ecostratigraphic zonation based

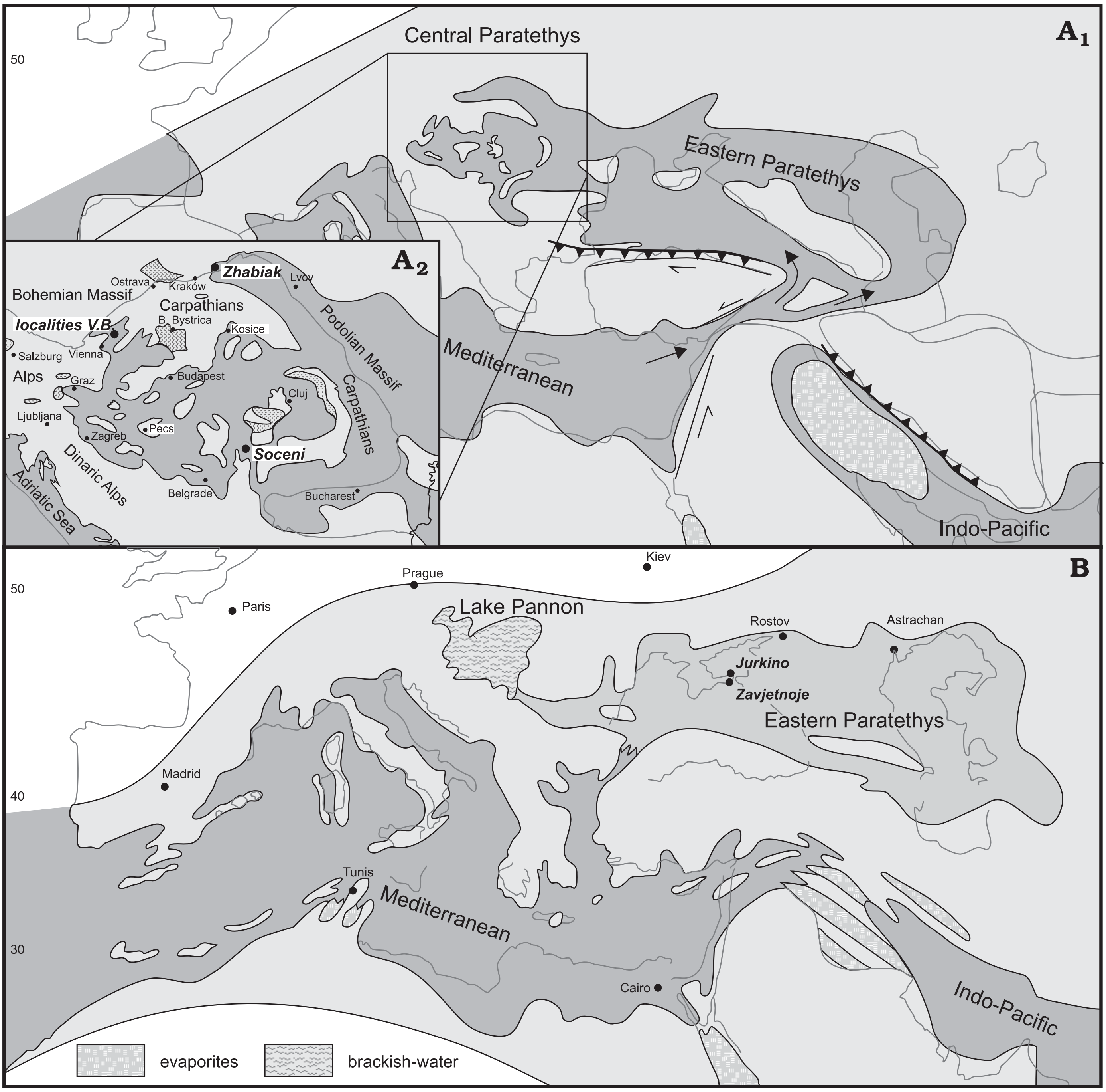

Fig. 1. Volhynian and Bessarabian paleogeography of the Paratethys. **A**. Middle Miocene: Early Sarmatian (Volhynian), after Rögl (1998). Entire Paratethys (A$_1$), close-up of the Central Paratethys (A$_2$). **B**. Late Miocene (late Bessarabian), after Rögl and and Steininger (1984).

on molluscs and benthic foraminifera, used solely for Sarmatian deposits sensu stricto of the Central Paratethys (Papp 1954, 1956; Rögl 1998; Harzhauser and Piller 2004b).

Based on the mollusc fauna, Papp (1956) differentiated the Sarmatian sensu stricto into 5 horizons (Papp and Seneš 1974):

(1) *Mohrensternia* Zone: This eco-biozone is the basal part of the Sarmatian succession. It is defined by a fauna of relatively small-bodied taxa, dominated by certain species of the genera *Mohrensternia* as well as small cardiid bivalves, *Abra*, small *Ervilia*, and some *Mactra* (< 2 cm).

(2) Lower *Ervilia* Zone: This eco-biozone is defined by deposits containing different genera of *Ervilia* and *Potamides* as well as large cardiids.

(3) Upper *Ervilia* Zone: This eco-biozone shows the most diverse mollusc fauna of the Sarmatian. Different species of large *Ervilia* and cardiids such as *Obsoletiforma vindobonensis* are typical.

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Table 3. Five most common species found per locality (in percent).

	Siebenhirten	Kettlasbrunn	Hauskirchen	Nexing	Soceni	Zhabiak	Jurkino	Zavjetnoje
Cerithium rubiginosum	–	–	1.5–46.3	–	–	–	–	–
Potamides disjunctus	–	–	1.9–3.4	–	–	–	–	–
Granulolabium bicinctum	0.0–81.2	–	0.2–7.2	16.8–28.1	20.0–21.4	–	–	–
Melanopsis impressa	–	–	–	–	4.0–10.5	–	–	–
Mohrensternia inflata	0.0–49.1	–	–	–	–	21.8–35.8	–	–
Mohrensternia styriaca	0.0–19.4	–	–	–	–	–	–	–
Mohrensternia pseudoangulata	–	–	–	–	–	0.4–18.4	–	–
Rissoa soceni	–	–	–	–	–	0.4–9.7	–	–
Hydrobia spp.	–	0.9–10.7	3.3–10.5	10–23.0	11.4–11.7	–	0–35.9	3.3–54.7
Pseudamnicola sp.	–	–	–	–	–	–	0–30.8	0–43.4
Pseudamnicola cyclostomoides	–	–	–	–	–	–	0–24.6	–
Akburunella akburunensis	–	–	–	–	–	–	0–7.6	–
Acteocina lajonkaireana	–	0.7–6.4	–	–	–	0–4.5	–	–
Musculus sarmaticus	–	–	–	–	–	–	–	0–28.9
Mytilaster volhynicus	–	–	–	–	5.3–13.0	–	–	–
Obsoletiforma vindobonensis	–	–	–	9.6–18.6	–	–	–	–
Mactra andrussowi	–	–	–	–	–	–	–	0–28.9
Abra reflexa	1.5–41.3	–	–	–	–	–	–	–
Donax dentiger	–	2.8–7.5	–	–	–	–	–	–
Ervilia dissita	0.0–22.1	7.5–34.5	3.1–86.1	11–23.2		34–46.2	–	–
Mytilopsis ramphophora	–	–	–	–	5.7–8.1	–	–	–
Venerupis tricuspis	–	45–76.3	–	12.7–24.0	–	–	0–16.1	1.2–36.9

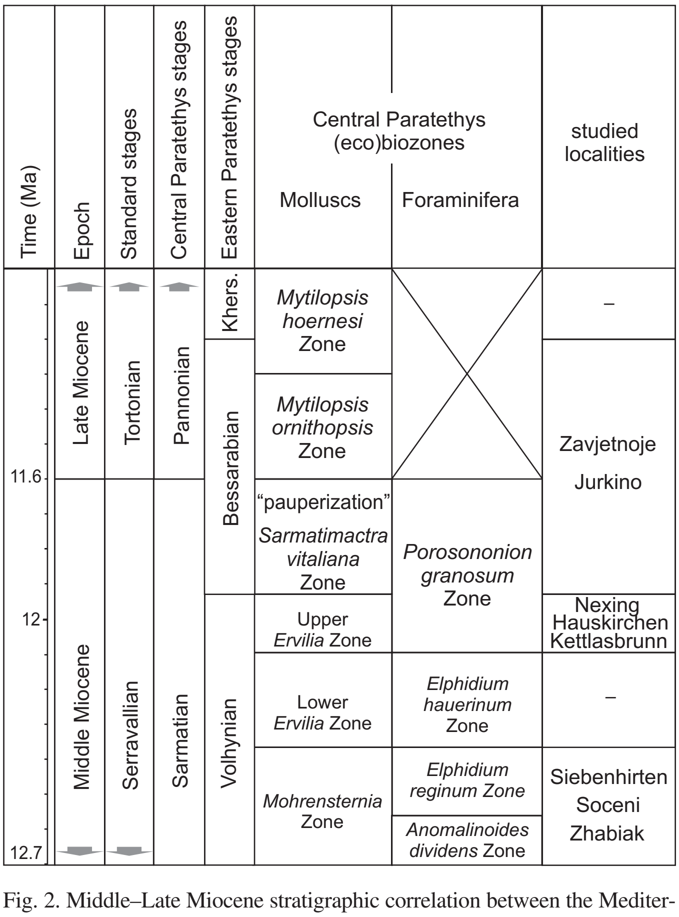

Fig. 2. Middle–Late Miocene stratigraphic correlation between the Mediterranean and Paratethys areas (modified after Harzhauser and Piller 2004b). Khers, Khersonian.

(4) *Mactra*-beds: Marked by the decline of some species (e.g., different species of *Ervilia* and *Cerithium*) in the *Sarmatimactra vitaliana* Zone. Large shells of *Sarmatimactra vitaliana* and *Venerupis tricuspis* are typical.

(5) Pauperization Zone: This eco-biozone is characterised by small cardiid bivalves, *Cerithium hartbergensis* as well as some rudimentary species of *Venerupis*, *Donax* and solenids, along with rare species of *Cryptomactra*.

Subsequently, the term Sarmatian was also used for deposits formed in the Eastern Paratethys of Eastern Europe and Asia. In this area, the term Sarmatian has to be abandoned and must be replaced by the regional stages Volhynian, Bessarabian, and Khersonian (Harzhauser and Piller 2004a, b). Of these, only the Volhynian and the lower Bessarabian have marine equivalents in the Central Paratethys (Papp and Seneš 1974; Piller and Harzhauser 2005) (Fig. 2).

Localities

Four localities were sampled in the northern Vienna Basin (Siebenhirten, Kettlasbrunn, Hauskirchen, and Nexing; Fig. 5A). Descriptions and stratigraphic correlations are presented in Harzhauser and Piller (2004a, b, 2010). The 11-m-thick Siebenhirten section (12.7–12.4 Ma) is located approximately 5 km northwest from Mistelbach and belongs to the regional *Mohrensternia* Zone (Harzhauser and Piller 2004b). The basal part is represented by fluvial gravel which was shed through a drainage system of the North Alpine Foreland Basin (NAFB) into the northwestern Vienna Basin during a sea level low

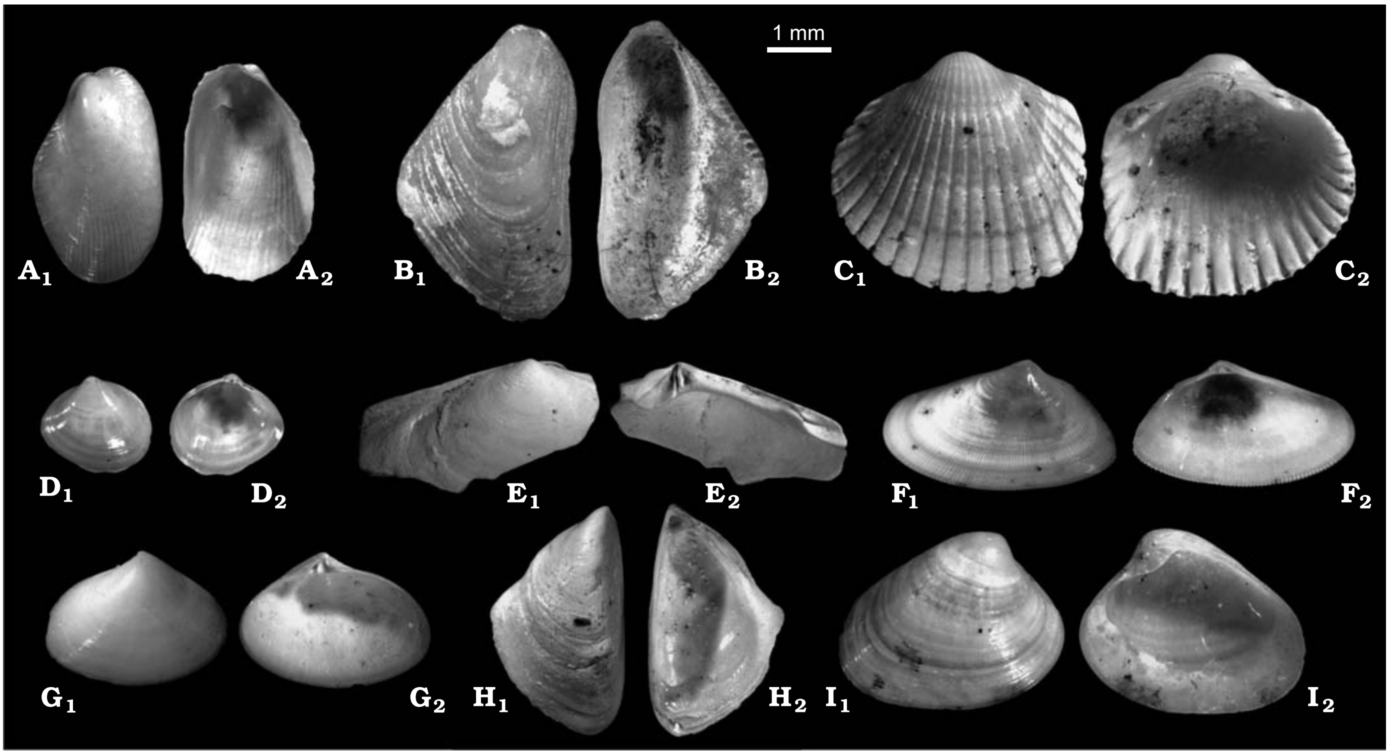

Fig. 3. Most abundant taxa of bivalves from outcrops of the ancient Central Paratethys (Siebenhirten, Kettlasbrunn, Nexing, Hauskirchen, Soceni Politioană, and Zhabiak) and from outcrops of the ancient Eastern Paratethys (Jurkino and Zavjetnoje). **A**. NHMW-2011/0272/0001, *Musculus sarmaticus* (Gatuev, 1916), Zavjetnoje, Bessarabian. **B**. NHMW-2011/0268/0001, *Mytilaster volhynicus* (Eichwald, 1829), Kettlasbrunn, Upper *Ervilia* Zone. **C**. NHMW-2011/0268/0002, *Obsoletiforma vindobonensis Laskarev*, 1903, Kettlasbrunn, Upper *Ervilia* Zone. **D**. NHMW-2011/0272/0002, *Mactra andrussowi* Kolesnikov, 1925, Zavjetnoje, Bessarabian. **E**. NHMW-2011/0271/0001, *Abra reflexa* (Eichwald, 1830), Jurkino, Bessarabian. **F**. NHMW-2011/0268/0003, *Donax dentiger* Eichwald, 1830, Kettlasbrunn, Upper *Ervilia* Zone. **G**. NHMW-2011/0269/0001, *Ervilia dissita* (Eichwald, 1830), Hauskirchen, Upper *Ervilia* Zone. **H**. NHMW-2011/0266/0001, *Mytilopsis ramphophora* (Brusina, 1892), Soceni Politioană, *Mohrensternia* Zone. **I**. NHMW-2011/0269/0002, *Venerupis tricuspis* Eichwald, 1830, Hauskirchen, Upper *Ervilia* Zone.

stand at the Badenian/Sarmatian boundary (Mandic et al. 2008). The subsequent flooding of the NAFB during the *Mohrensternia* Zone and the abrupt transgression led to the deposition of marine clay, from which our samples were taken (Fig. 5B).

The sections Kettlasbrunn (11.9 Ma), Hauskirchen, and Nexing (12.1–11.9 Ma) belong to the regional Upper *Ervilia* Zone. The chronostratigraphic calibrations follow the proposed relation to isotopic events (Harzhauser and Piller 2004b). During that time, the northwestern margin of the Vienna Basin was covered by extensive ooid shoals, with sandy beaches, tidal channels and dunes of ooids and shell-hash. At Kettlasbrunn, 5 km east of Mistelbach (Fig. 5A), such unlithified sand of loose shell-hash is exposed. The lower part of the 3-m-thick section consists of 2 m of fine to medium sand containing cross-bedded sand layers with bivalves, overlain by about 1.30 m of oolitic sandstone. The samples from Kettlasbrunn were all taken from the lower part of the section (shown in Fig. 5C).

Hauskirchen is situated approximately 15 km northeast of Mistelbach (Fig. 5A). Papp (1954, 1956) placed the mollusc assemblages of this locality into the Upper *Ervilia* Zone and proved this by the occurrence of the indicative foraminifera *Porosononion granosum*. The 3-m-thick section starts with 1.6 m of fine unlithified sand containing dispersed bivalves and gastropods. Upsection, the sand is increasingly replaced by unlithified oolitic sand and finally by a more than 1-m-thick bed of massive oolitic limestone. While sample Hauskirchen 4 was taken from the lower part of the section, samples Hauskirchen 1, 2, and 3 derive from the overlying 0.5 m of oolitic sand (Fig. 5D).

Nexing, the holostratotype of the Sarmatian stage, is located approximately 10 km southeast from Mistelbach (Fig. 5A). The deposits are dated as Upper *Ervilia* Zone and lowermost *Sarmatimactra vitaliana* Zone (Harzhauser and Piller 2010). The section is outstanding for its sedimentological features, with huge shell dunes consisting of up to 81% of shell hash of marine bivalves and gastropods (Fig. 5E). According to Harzhauser and Piller (2010), the 13-m-high fore-sets are part of a flood tidal-delta.

In the Pannonian Basin System, samples were taken in the Politioană valley of Soceni, located in northwest Romania (350 km northwest of Bucharest) (Fig. 6). The mollusc fauna derives from a 5.5-m-thick succession of siliciclastic deposits of Early Sarmatian age (12.5 Ma; *Mohrensternia* Zone) which transgress on the crystalline basement. Intense synsedimentary reworking is indicated by bryozoan-limestone clasts (Fig. 7). The mollusc fauna, too, represents a

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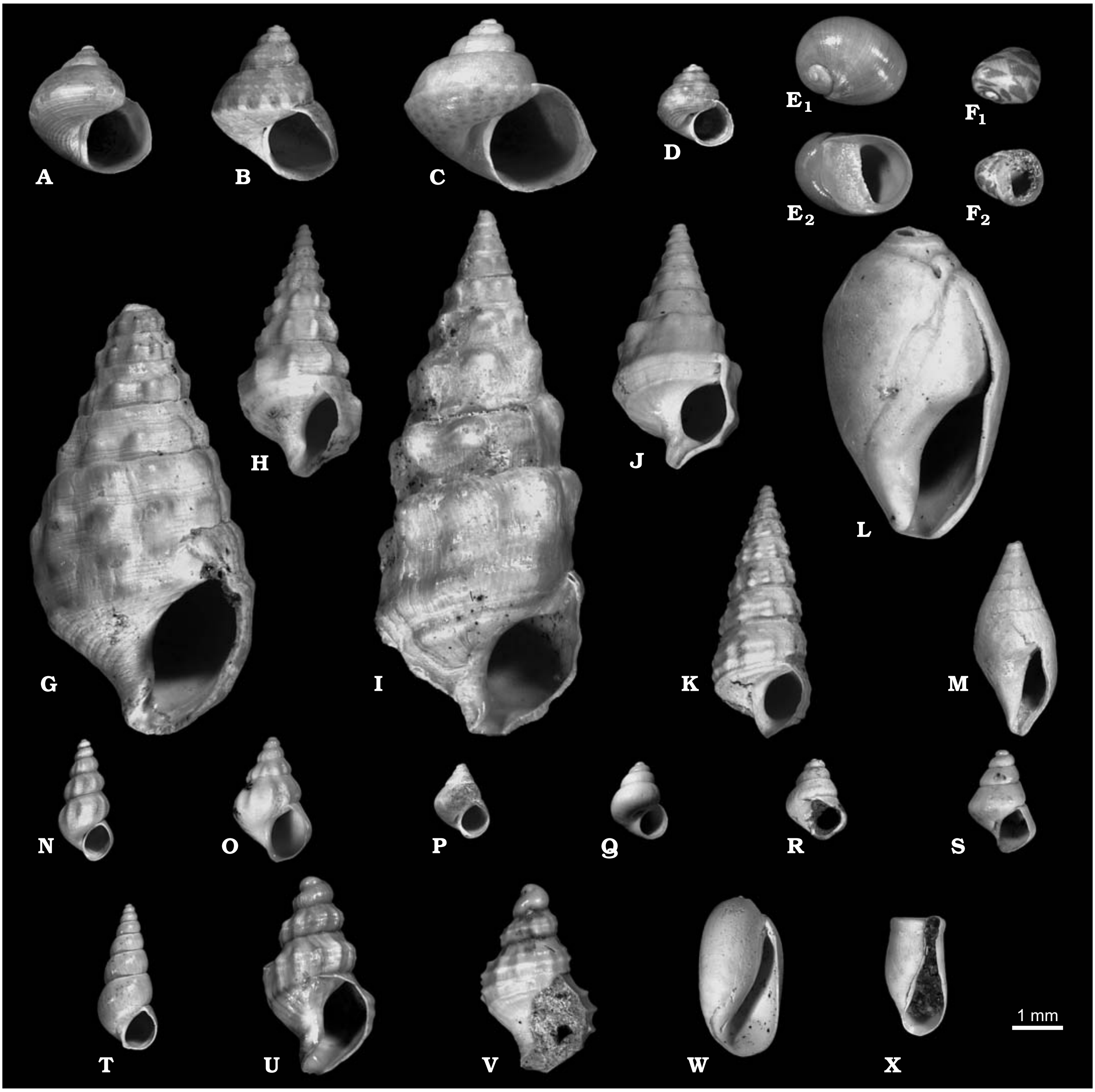

Fig. 4. Abundant taxa of gastropods from outcrops of the ancient Central Paratethys (Siebenhirten, Kettlasbrunn, Nexing, Hauskirchen, Soceni Politioană, and Zhabiak) and from the ancient Eastern Paratethys (Jurkino and Zavjetnoje). **A**. NHMW-2011/0269/0003, *Gibbula angulata* (Eichwald, 1853), Hauskirchen, Upper *Ervilia* Zone. **B**. NHMW-2011/0266/0002, *Gibbula banatica* (Jekelius, 1944), Soceni Politioană, *Mohrensternia* Zone. **C**. NHMW-2011/0271/0002, *Gibbula urupensis* (Uspenski, 1927), Jurkino, Bessarabian. **D**. NHMW-2011/0272/0003, *Gibbula* sp. 1, Zavjetnoje, Bessarabian. **E**. NHMW-2011/0266/0003, *Theodoxus politus* Jekelius, 1944, in apical (E_1) and apertural (E_2) views, Soceni Politioană, *Mohrensternia* Zone. **F**. NHMW-2011/0266/0004, *Theodoxus soceni* Jekelius 1944, in apical (F_1) and apertural (F_2) views, Soceni Politioană, *Mohrensternia* Zone. **G**. NHMW-2011/0266/0005, *Cerithium rubiginosum* (Eichwald, 1853), adult, Soceni Politioană, *Mohrensternia* Zone. **H**. NHMW-2011/0269/0004, *Cerithium rubiginosum* (Eichwald, 1853), juvenile, Hauskirchen, Upper *Ervilia* Zone. **I**. NHMW-2011/0266/0006, *Granulolabium bicinctum* (Brocchi, 1814), adult, Soceni Politioană, *Mohrensternia* Zone. **J**. NHMW-2011/0266/0007, *Granulolabium bicinctum* (Brocchi, 1814), juvenile, Soceni Politioană, *Mohrensternia* Zone. **K**. NHMW-2011/0269/0005, *Potamides disjunctus* (Sowerby, 1831), Hauskirchen, Upper *Ervilia* Zone. **L**. NHMW-2011/0266/0008, *Melanopsis impressa* (Krauss, 1852), adult, Soceni Politioană, *Mohrensternia* Zone. **M**. NHMW-2011/0266/0009, *Melanopsis impressa* (Krauss, 1852), juvenile, Soceni Politioană, *Mohrensternia* Zone. **N**. NHMW-2011/0267/0001, *Mohrensternia pseudoangulata* Hilber, 1897, Siebenhirten, *Mohrensternia* Zone. **O**. NHMW-2011/0267/0002, *Mohrensternia inflata* (Andrzejowsky, 1835), Siebenhirten, *Mohrensternia* Zone. **P**. NHMW-2011/0266/0010, *Pseudamnicola sarmatica* Jekelius, 1944, Soceni Politioană, *Mohrensternia* Zone. **Q**. NHMW-2011/0272/0004, *Pseudamnicola cyclostomoides* (Sinzov, 1880), →

mixture of shallow marine taxa with freshwater molluscs and even rare terrestrial gastropods (Jekelius 1944).

On the Volhyno-Podolian Plate (Galets'kyi 2007), sediments of the Zhabiak locality, located in the Ukraine, 150 km east of the Polish border, were studied (Fig. 6). The section comprises Badenian and Lower Sarmatian deposits. The uppermost 7 m of the 24-m-thick section are of Sarmatian age (12.7 Ma; *Mohrensternia* Zone) and comprise unlithified fine to coarse sand containing a microbialite-serpulid-bioherm. Upsection follow 3 m of dark grey to brown clay of Pleistocene age (Fig. 8). Samples were taken from tempestitic shell beds.

In the Indol-Kuban Basin, sediments of the Jurkino and Zavjetnoje localities were studied. They belong to the western part of the Eastern Paratethys. Both are located in the eastern part of the Crimea Peninsula (Kertch, Ukraine; Fig. 6) and are part of the Indol-Kuban Basin (Galets'kyi 2007). The deposits of both sections are of Bessarabian age (11.5–11.2 Ma) (Fig. 2). Marl and oolitic limestone, along with diatomite and diatomitic marl predominate (Andrussow 1911), and both sections are interpreted here as shallow to moderately deep sublittoral. The Jurkino section has a thickness of about 50 m of diatomitic marls, silts and cross-bedded oolite sands (Fig. 9). The mollusc samples (Jurkino 1 and 2a–c) are taken from the lowermost 2 m of the log. Sample Jurkino 7 was taken from scattered shell beds of the topmost clayey part (48 m). The approximately 32.7-m-thick section of Zavjetnoje (Fig. 10) alternates between clay, silt, and fine sand. Towards the top, the sedimentation becomes increasingly diatomitic. The whole section contains numerous shell beds.

Material and methods

Sample preparation.—The samples from Zhabiak (Ukraine) and Soceni (Romania) were taken in 2001. Samples from the Crimea Peninsula (Ukraine, Jurkino and Zavjetnoje) and from the Vienna Basin (Hauskirchen, Nexing, Siebenhirten, and Kettlasbrunn) were taken in 2008. For each outcrop a log was provided and mollusc samples collected.

The sediment was sieved with 4, 2, and 1 mm size meshes, air dried, and split to a workable size. Thirty-two samples, with a median sample size of 1061.5 specimens, were studied. Molluscs were picked under a binocular microscope. This yielded 47,840 shells representing 13 species from 13 bivalve genera, and 71 species from 26 gastropod genera. The taxonomy and systematics are in accordance with the determinations of Friedberg (1911–1928), Kolesnikov (1935), Simonescu and Barbu (1940), Jekelius (1944), Papp (1954, 1956, 1974b), Kojumdgieva (1969, 1987), Švagrovský (1971), Harzhauser and Kowalke (2004), Kowalke and Harzhauser (2004), Nevesskaja et al. (1993), and Bouchet and Rocroi (2005).

Statistical methods.—The statistical analyses were performed with the program PAST version 1.82 (Hammer et al. 2001). All analyses are based on arcsine-root transformed percentages of the species within each sample (Linder and Berchtold 1976).

To detect hierarchical groupings within the data set, we applied paired group cluster analysis using the Bray-Curtis similarity index. All species represented by less than 20 individuals were removed from the data set. Also, sample Jurkino 7 was not included because of its low number of species (n = 1).

To test the significance of the differences between localities, analysis of similarity (ANOSIM) was applied, based on the Bray-Curtis similarity coefficient (Bray and Curtis 1957; Clarke and Warwick 1994). Several palaeoecological analyses have used ANOSIM to measure temporal turnover in composition (e.g., Casanovas-Vilar and Agusti 2007; Zuschin et al. 2007; Sallan and Coates 2010). Global R values were always highly significant, but for individual comparisons the significance values can often be low, because of few replicates in each group. We therefore also used the pairwise R values, which give an absolute measure of how separated the groups are. R values can range from 0 (indistinguishable) to 1 (all similarities within groups are less than any similarity between groups) (Clarke and Gorley 2001). R values > 0.75, groups well separated; R values > 0.5, groups overlapping but clearly different; R values > 0.25, groups strongly overlapping; R values < 0.25, groups barely separable (Tables 4–6). As the number of samples per group is different, however, variable dispersion can also be a reason for significant R values of ANOSIM (Anderson 2001).

Results

All studied localities are strongly dominated by just a few species (Table 3, Figs. 11, 12), but samples cluster according to region and stratigraphy (Fig. 13). At a similarity level of 0.3 the Bessarabian samples of the Crimean region form one cluster and the Volhynian samples two clusters (V1, V2). In cluster V2, all samples are from the *Mohrensternia* Zone, but they are from different regions (Vienna Basin and western Ukraine). In cluster V1, nearly all samples are from the Vienna Basin and two are from Soceni (Romania). Most samples here are from the Upper *Ervilia* Zone, but three are from the *Mohrensternia* Zone (Siebenhirten 3, both samples from Soceni).

Most species are restricted to stages and/or regions, but some have wider distributions. Species occurring in all regions and all stages are the gastropods *Acteocina lajon-*

Zavjetnoje, Bessarabian. **R**. NHMW-2011/0271/0003, *Pseudamnicola* sp., Jurkino, Bessarabian. **S**. NHMW-2011/0271/0004, *Pseudamnicola* sp. 2., Jurkino, Bessarabian. **T**. NHMW-2011/0266/0011, *Hydrobia* sp., Soceni Politioană, *Mohrensternia* Zone. **U**. NHMW-2011/0272/0005, *Akburunella akburunensis* (Andrussow, 1902), Zavjetnoje, Bessarabian. **V**. NHMW-2011/0272/0006, *Akburunella akburunensis* (Andrussow, 1902), Zavjetnoje, Bessarabian. **W**. NHMW-2011/0268/0004, *Acteocina lajonkaireana* Basterot, 1825, Kettlasbrunn, Upper *Ervilia* Zone. **X**. NHMW-2011/0271/0005, *Retusa truncatula* (Bruguière, 1792), Jurkino, Bessarabian.

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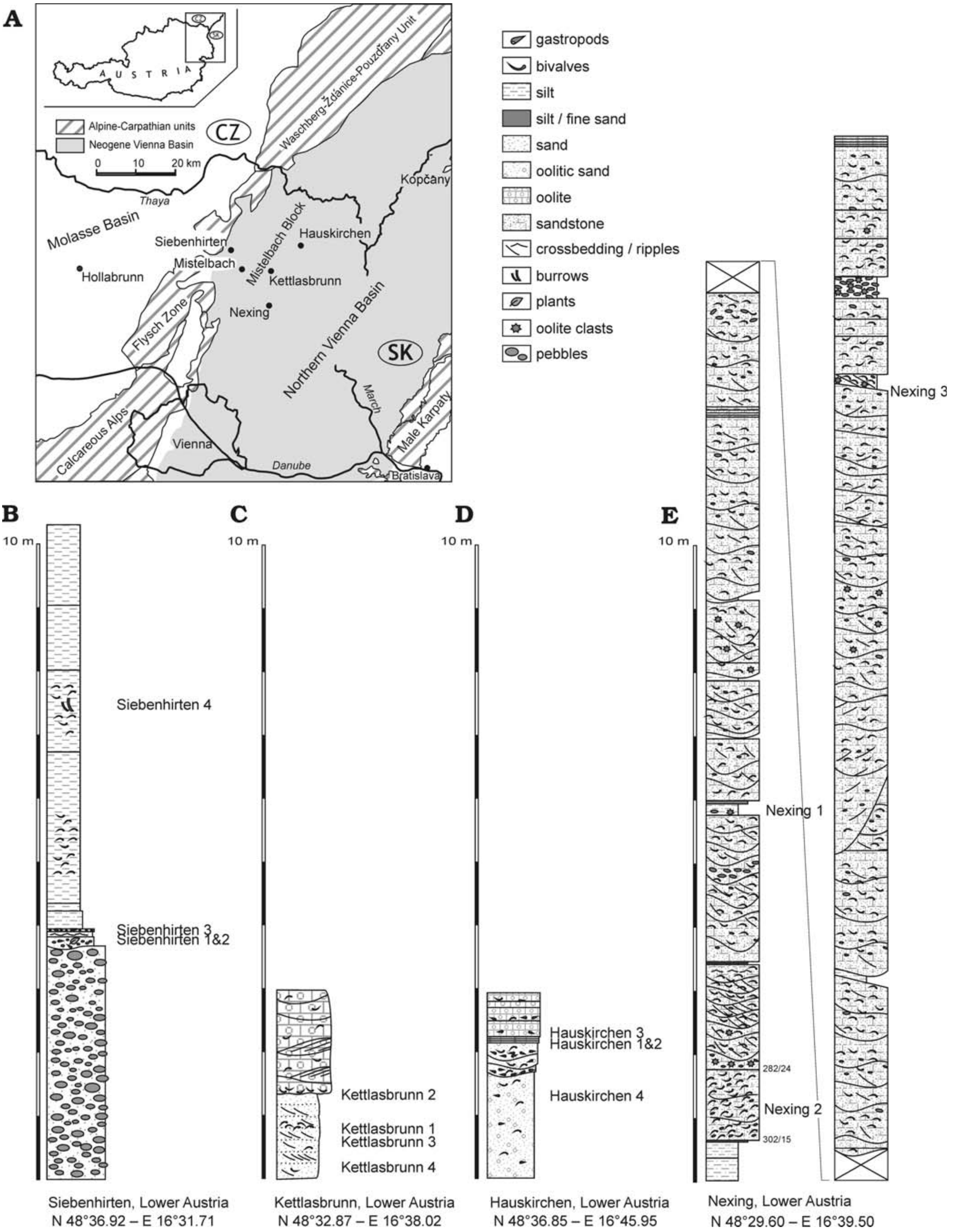

Fig. 5. **A**. Northern Vienna Basin (grey area) within Alpine-Carpathian units and positions of the localities Siebenhirten, Kettlasbrunn, Hauskirchen and Nexing. **B–E**. Logs of the localities Siebenhirten (**B**), Kettlasbrunn (**C**), Hauskirchen (**D**), Nexing (**E**) (modified after Harzhauser and Piller 2004b).

kaireana and *Hydrobia* spp., and the bivalves *Mytilaster volhynicus*, *Venerupis tricuspis*, *Musculus sarmticus*, and *Blinia pseudolaevigata*. Some species are restricted to the Volhynian but occur in several regions. These include the gastropods *Granulolabium bicinctum*, *Mohrensternia* spp., and *Cerithium rubiginosum* and the bivalves *Ervilia dissita* and *Abra reflexa*. The gastropod *Retusa truncatula* is an outlier because it occurs with low numbers in few samples from different regions (Vienna Basin, western Ukraine). In accordance with these distinct distribution patterns, the R-mode cluster A is characterised by species that are restricted to samples from the Bessarabian of the Crimean region. Exceptions are *Musculus sarmaticus* and *Blinia pseudolaevigata*. Species of cluster B are most widespread in Volhynian samples, mostly from the Vienna Basin, although some occur in Bessarabian samples as well (*Acteocina lajonkaireana*, *Hydrobia* spp., and *Venerupis tricuspis*). Cluster C is characterised by species that are rare and only occur in samples from Soceni (Romania); an exception is *Gibbula banaticum*, which was also found in samples from Zhabiak (western Ukraine). Species of Cluster D are largely restricted to Volhynian samples from different regions (Vienna Basin, western Ukraine, and Romania).

The three Q-mode clusters represent different shallow-water environments of the Volhynian and Bessarabian and are characterised by distinct biofacies. The Volhynian cluster V1 includes mostly samples from well-agitated shores of the Vienna Basin and from Soceni (Romania) and is characterised by the *Granulolabium–Venerupis–Ervilia* assemblage. The taxa of this assemblage are typical inhabitants of tidal flats and shallow subtidal sediments. Within this cluster the samples from Soceni (Romania) stand out because they include a quite high abundance of taxa which tolerate freshwater like *Melanopsis impressa*, *Theodoxus* spp., and *Mytilopsis ramphophora* (Fig. 13: 1b). The Volhynian cluster V2 comprises samples from a muddy foreshore of Zhabiak (western Ukraine) and Siebenhirten (Vienna Basin). These samples are characterised by the *Granulolabium–Ervilia–Mohrensternia* assemblage (Fig. 13: 2). These taxa are inhabitants of a muddy bottom, and *Mohrensternia* indicates a phytal cover. Within this cluster the two samples from Siebenhirten have higher abundances of *Granulolabium bicinctum*, while the Zhabiak samples show higher abundances of *Ervilia dissita* and *Mohrensternia* spp.

The Bessarabian cluster includes samples from a shallow to moderately deep sublittoral of Zavjetnoje and Jurkino (Crimean region). This cluster is characterised by the *Hydrobia–Venerupis–Pseudamnicola* assemblage (Fig. 13: 3). *Musculus sarmaticus* and *Mactra andrussowi* are also quite abundant within these samples. These species are typical inhabitants of sandy shallow to moderately deep sublittoral sediments.

Both Bessarabian localities (Jurkino and Zavjetnoje) are significantly different from almost all Volhynian localities (Table 4). Among the Volhynian localities, overlapping assemblages are present in the Vienna Basin between Siebenhirten and Nexing, between Siebenhirten in the Vienna Basin and Zhabiak in the western Ukraine, as well as between Siebenhirten (Vienna Basin) and Soceni (Romania). In accordance with these results, the regional comparison shows overlapping assemblages of the Vienna Basin with western Ukraine and Romania. All other regions differ strongly from each other (Table 5). Among stratigraphic units, the samples from the *Mohrensternia* Zone (Vienna Basin, Romania, western Ukraine) and the Upper *Ervilia* Zone (Vienna Basin) have overlapping but still significantly different assemblages. The Bessarabian, however, differs strongly from both Volhynian biozones (Table 6).

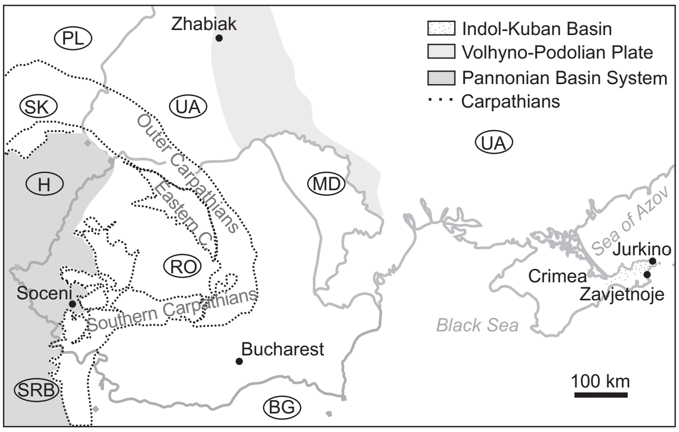

Fig. 6. Geographic and geological position of the outcrops Soceni (Romania), Zhabiak, Jurkino, and Zavjetnoje (Ukraine).

Discussion

Background.—Because of the absence of stenohaline biota, such as radiolarians, planktic foraminifera, corals and echinoderms, the Sarmatian stage was interpreted in the Central Paratethys as transitional between the marine Badenian and the lacustrine Pannonian stages (Papp 1954, 1956; Turnovsky 1963; Bretenská 1974; Seneš 1974; Steininger and Wessely 2000). Brackish character of the Sarmatian Sea was also suggested based on fibre cement and the common occurrence of ooids (Pisera 1996). In contrast, Jámbor (1978) assumed normal to hypersaline conditions based on the presence of evaporites within Sarmatian deposits. More recently, Piller and Harzhauser (2005) documented a complex succession, starting with a mixohaline and eutrophic early Sarmatian Sea that became replaced by a marine to hypersaline, carbonate-oversaturated sea during the late Sarmatian. This process coincides with a switch in sedimentation from siliciclastic sediments to carbonate deposits (Piller and Harzhauser 2005) and explains the strongly changing composition of the endemic mollusc fauna. Interrupted seaways into the Mediterranean/Indo-Pacific (Rögl 1998; Piller and Harzhauser 2005), caused by the sea level drop at the Badenian/Sarmatian boundary, prohibited the re-immigration of the stenohaline biota. Due to an opening of a seaway into the Mediterranean Sea, the late

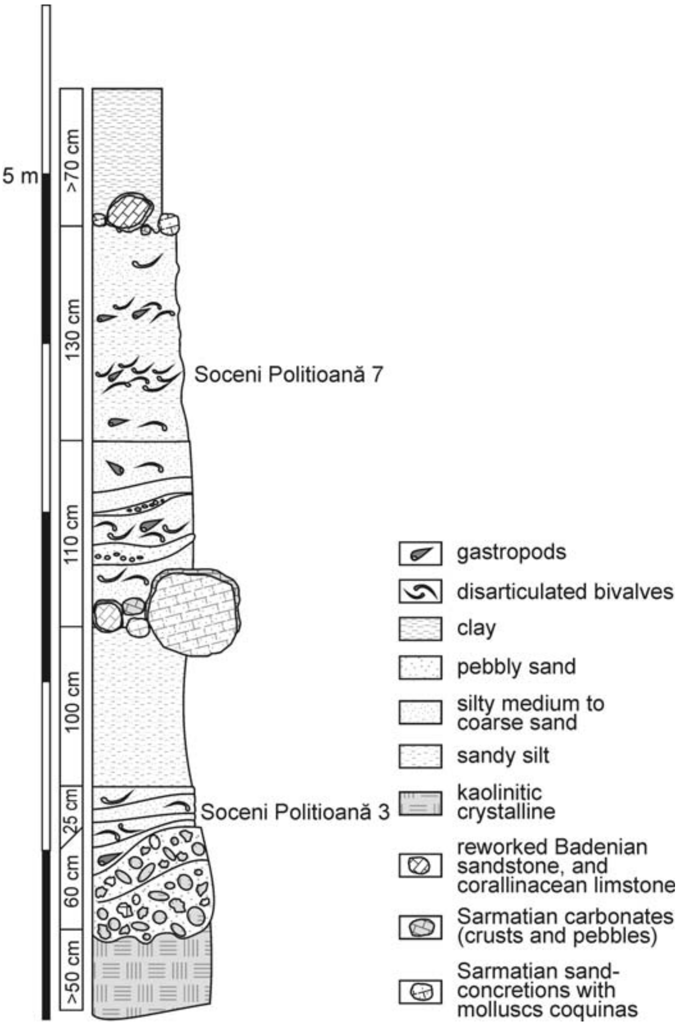

Fig. 7. Log of Soceni-Politioană, Romania (Pannonian Basin).

Sarmatian Sea ranged from fully marine to hypersaline conditions with a highly productive carbonate factory (oolite shoals, mass occurrence of thick-shelled molluscs and larger foraminifera) (see Piller and Harzhauser 2005). Moreover, within almost isolated systems, molluscs (especially gastropods) typically undergo conspicuous radiations reflecting habitat- or biotic complexity (Michel 1994). Several endemic radiations within the Paratethys occurred during the Neogene (Geary 1990), and Papp (1954) was among the first to use molluscs to arrange a biostratigraphical zonation of Sarmatian deposits from the Central Paratethys. So far, however, we lack any quantitative comparison of molluscan assemblages from the Central and Eastern Paratethys or a palaeoenvironmental interpretation.

Spatial and temporal signals.—In our dataset, the samples from Jurkino and Zavjetnoje are of Bessarabian age and from the Crimean region; they are therefore temporally and spatially strongly separated from all other samples. Within the Bessarabian / Crimean cluster, the samples group according to localities (Fig. 13).

Among the Volhynian localities, samples cluster roughly according to biozones (*Mohrensternia* Zone versus Upper *Ervilia* Zone), but the samples from Soceni and one sample from Siebenhirten are an exception. They belong to the *Mohrensternia* Zone, but group among the localities of the Upper *Ervilia* Zone (which otherwise are all from the Vienna Basin). The gastropod *Mohrensternia* serves as the best example of a strong temporal signal because it combines samples from the Vienna Basin (Siebenhirten) and the western Ukraine (Zhabiak).

Palaeoenvironments.—Throughout the Volhynian and Bessarabian, coastal zones and shoals of the Paratethys were dominated by sandy shores and ooid formations whilst deeper marine settings are indicated by pelitic deposits. These lithologies are well documented in the studied sections. Despite these persistent lithofacies, the biofacies display considerably differences as shown in our analysis.

The three biofacies, as determined by the combination of the R-mode and Q-mode cluster analysis (Fig. 13), can be used to interpret three distinct palaeoenvironments. Well-agitated shores are characterised by the *Granulolabium–Venerupis–Ervilia* biofacies, a muddy foreshore by the *Granulolabium–Mohrensternia–Ervilia* biofacies and a shallow to moderately

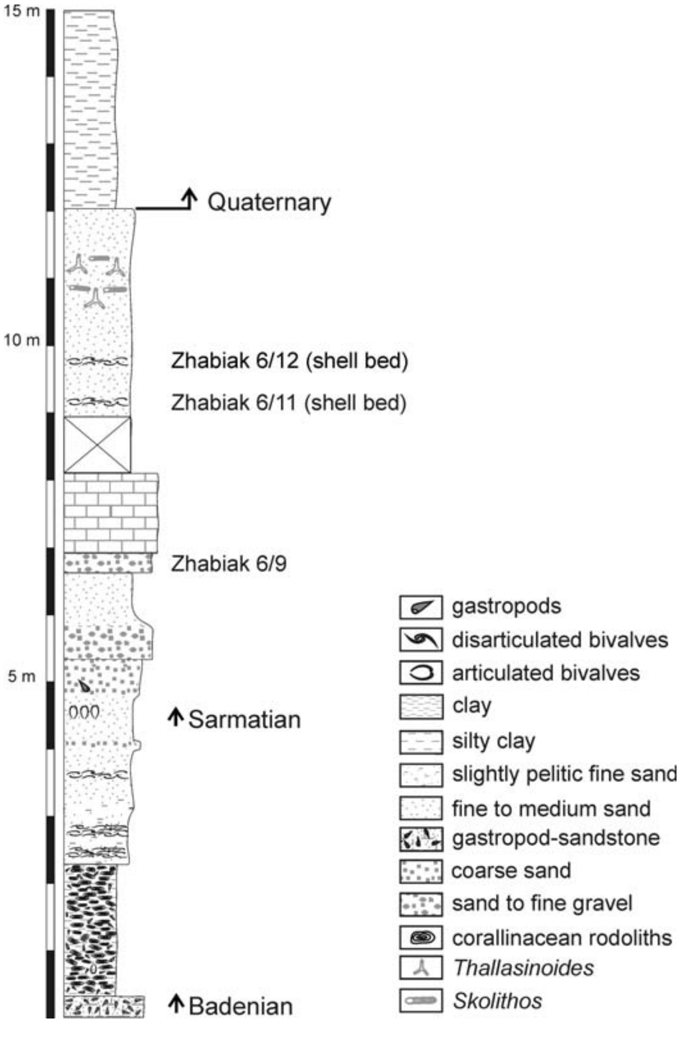

Fig. 8. Log of Zhabiak, western Ukraine (Volhyno-Podolian Plate).

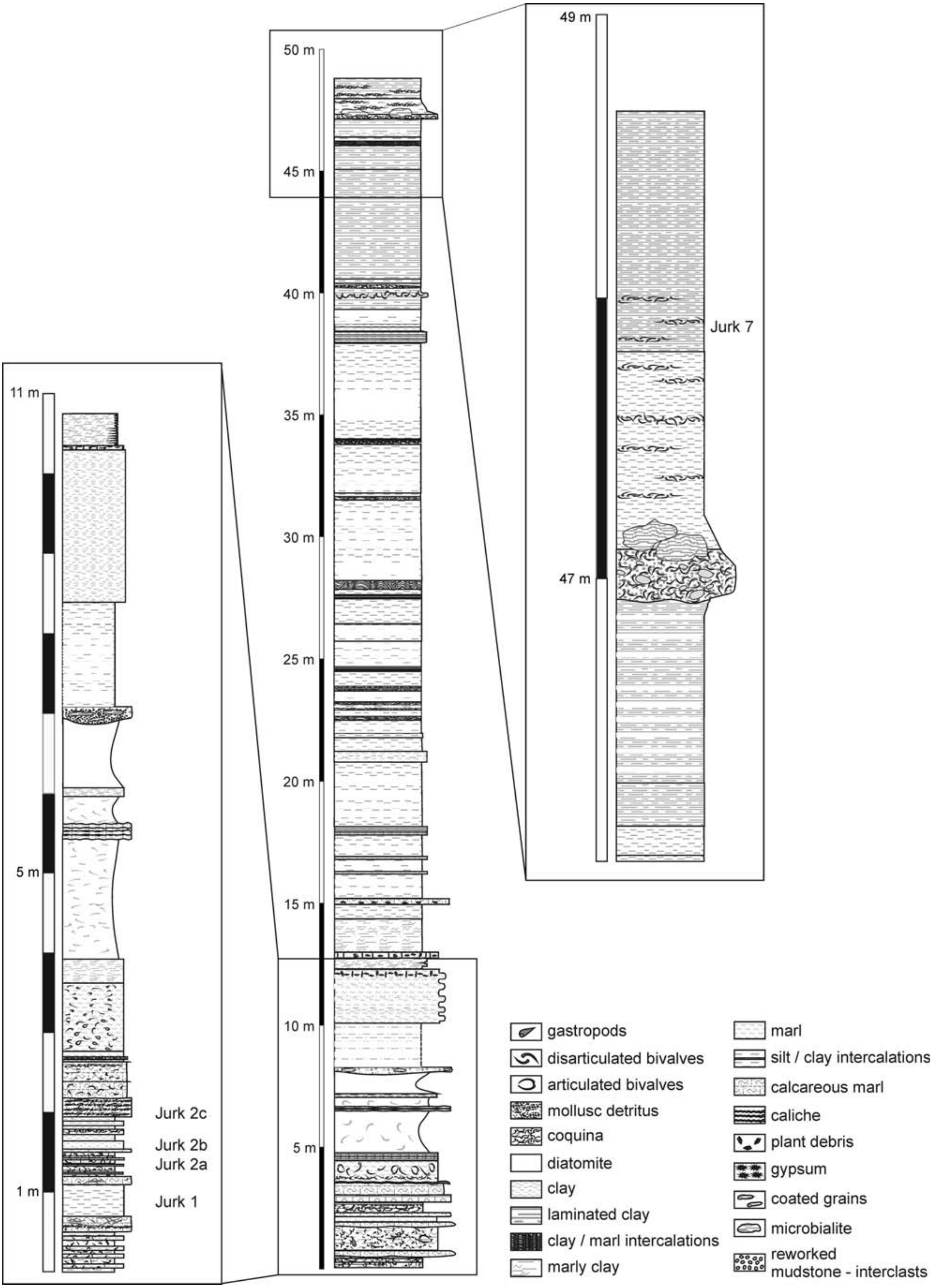

Fig. 9. Log of Jurkino, Peninsula Crimea, Ukraine (Indol-Kuban Basin).

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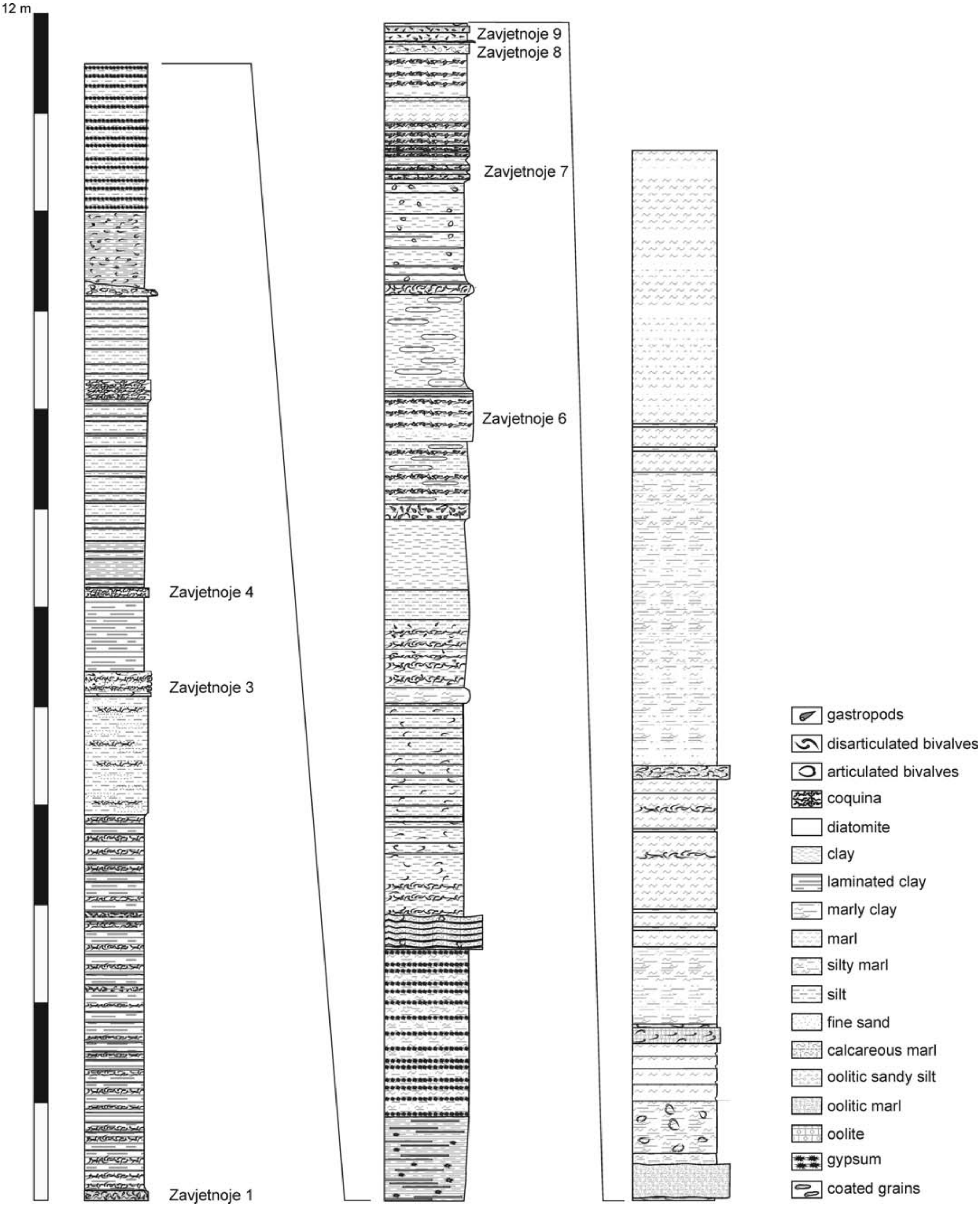

Fig. 10. Log of Zavjetnoje, Crimean Peninsula, Ukraine (Indol-Kuban Basin).

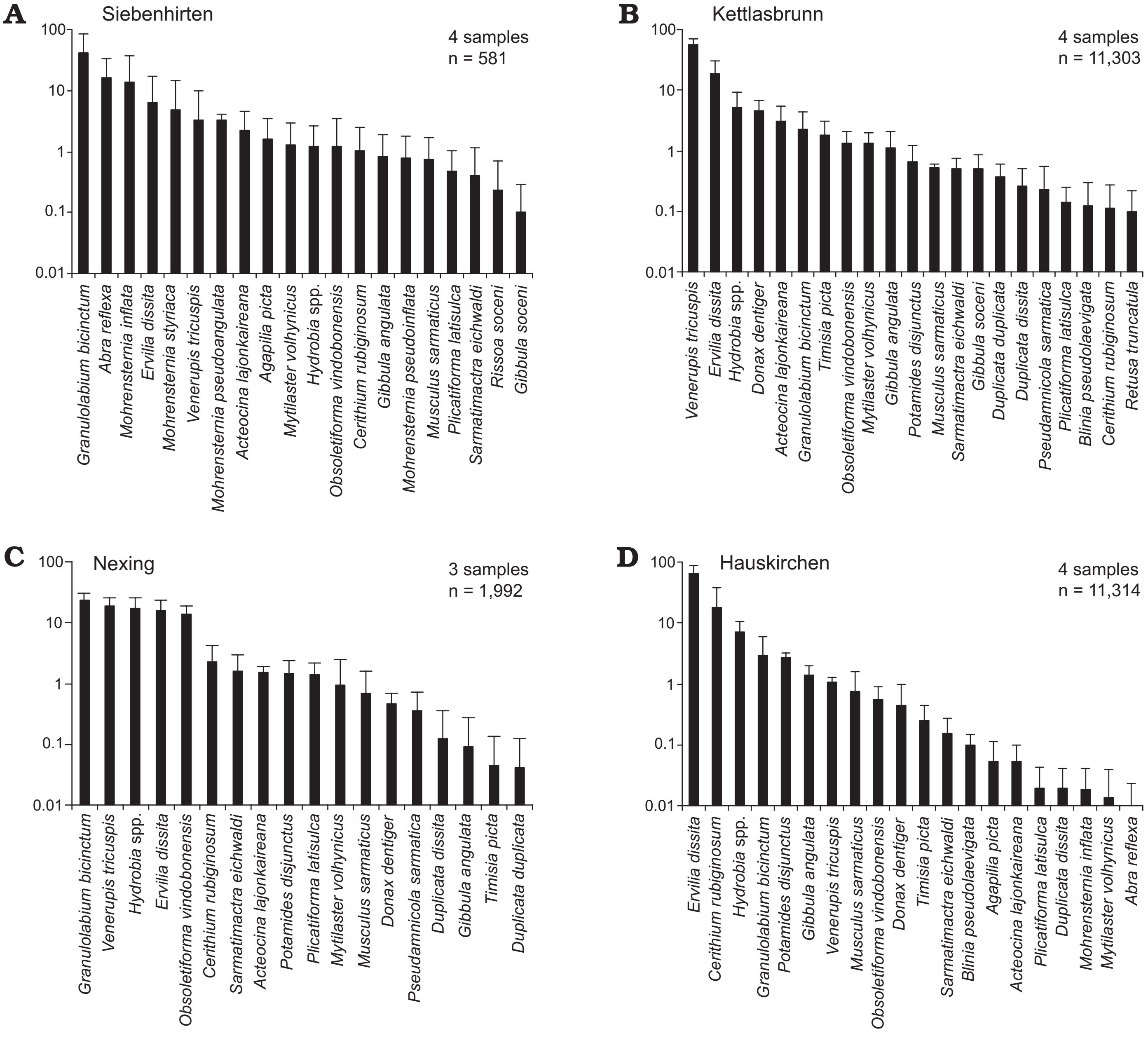

Fig. 11. Average percentage abundance of species with 95% confidence intervals on a logarithmic scale at the localities Siebenhirten (**A**), Kettlasbrunn (**B**), Nexing (**C**), and Hauskirchen (**D**).

deep sublittoral by the *Hydrobia–Venerupis–Pseudamnicola* biofacies. The well-agitated shore includes ooid shoal environments in the Vienna Basin (Nexing, Hauskirchen, Kettlasbrunn, Siebenhirten 3) and has high freshwater influx at Soceni, Romania. The muddy foreshore environment is phytal-associated, as indicated by the abundance of *Mohrensternia* within the samples of Zhabiak and Siebenhirten 4, and represents an intertidal mudflat channel at Siebenhirten 1 and 2. Not all biozones and regions of the Sarmatian Sea are covered within this study. Nevertheless, we suggest that these biofacies cover a wide and representative range of possible assemblage compositions of Sarmatian nearshore and shallow-water assemblages.

Species of the *Granulolabium–Venerupis–Ervilia* biofacies are mostly restricted to the Volhynian samples from the Vienna Basin (Kettlasbrunn, Nexing, Siebenhirten) and from Soceni (Romania) (Cluster V1, Fig. 13). Although the faunal compositions of these localities differ strongly from each other (Tables 3, 4), they share some environmental conditions. All samples from the wavy oolitic sand layers of Hauskirchen are characterised by a high abundance of *Ervilia dissita*, and they are also rich in *Cerithium rubiginosum* and *Hydrobia* spp., pointing to shallow-water conditions. Kettlasbrunn, Nexing, and sample Siebenhirten 3 are dominated by the bivalves *Ervilia dissita* and *Venerupis tricuspis*. The cross-bedded flood tidal deposits of Nexing consist of

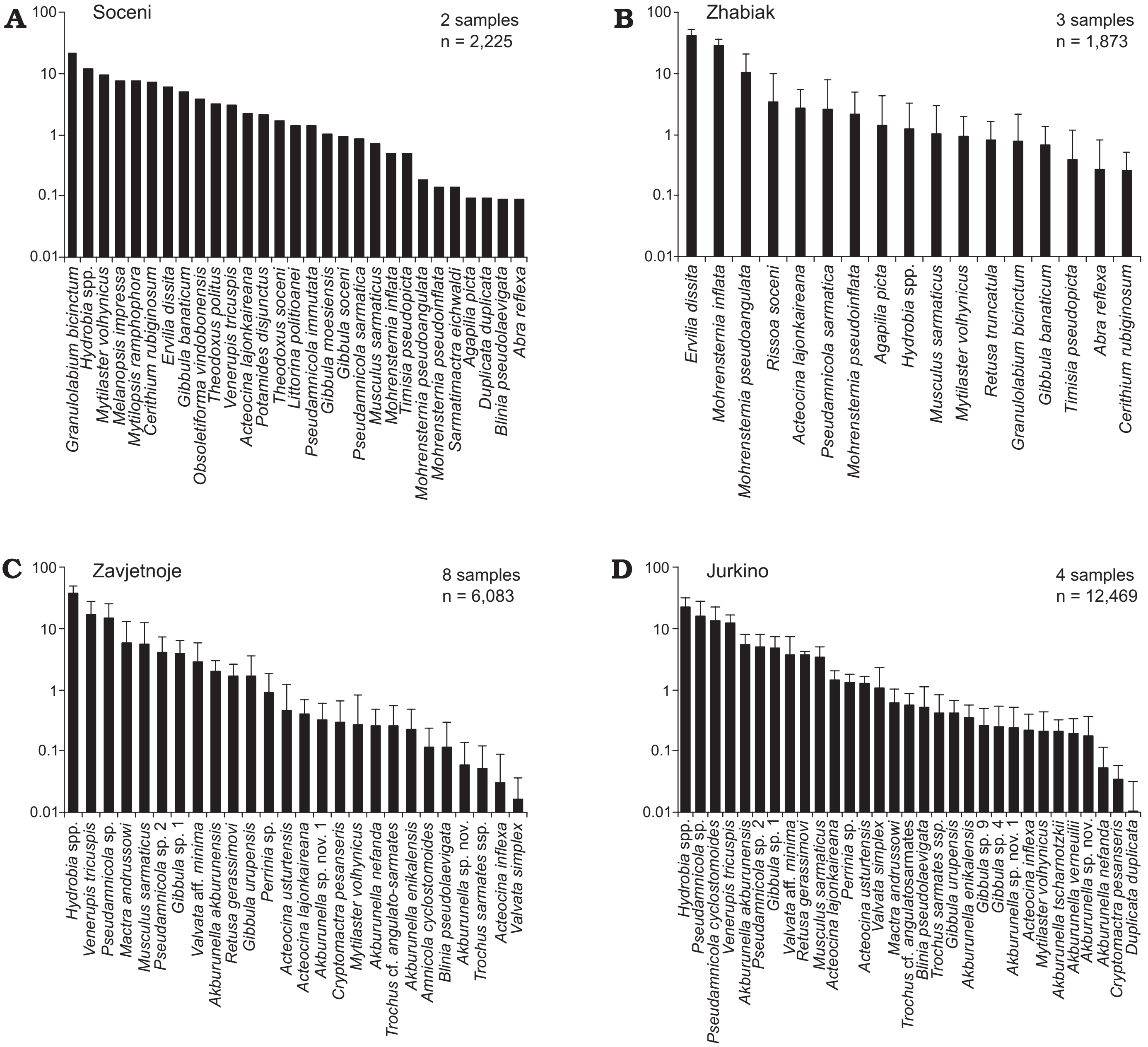

Fig. 12. Average percentage abundance of species with 95% confidence intervals on a logarithmic scale at the localities Soceni (**A**), Zhabiak (**B**), Zavjetnoje (**C**), and Jurkino (**D**).

transported shells; the numerous hydrobiid and batillariid gastropods seem to originate from intertidal environments, whilst the venerid, mesodesmatid, donacid, and cardiid bivalves are most probably taxa from the foreshore and shoreface (Harzhauser and Piller 2010). Sample Siebenhirten 3 bears high numbers of the infaunal bivalves *Abra reflexa* and *Ervilia dissita*, indicating a tidal flat environment between the underlying fluvial gravel and the overlying transgressive marine clay. Harzhauser and Piller (2004b, 2007) described the deposits of the Upper *Ervilia* Zone as carbonate, represented by oolites and coquina-dominated sands, which started to spread in nearshore settings and on shallow shoals. The oolite facies was also detected at Hauskirchen and Kettlasbrunn. Kowalke and Harzhauser (2004) suggest that the *Mohrensternia* communities became replaced by *Cerithium*-dominated assemblages at that time. This fits well to the samples from Hauskirchen, which are characterised by the high abundance of the gastropod *Cerithium rubiginosum*. Thus, sedimentology and the mollusc assemblages indicate a shallow coastal habitat in carbonate-oversaturated marine water of a well-agitated ooid shoal. The samples from the tempestitic shell beds at Soceni are characterised by intertidal species (*Granulolabium bicinctum*) and taxa which tolerate freshwater (*Hydrobia*, *Melanopsis*, *Mytilaster*). Several species/genera, which cluster at branch C of the R-mode cluster analysis (Fig. 13), tolerate freshwater influx. The tempestites indicate a well-agitated shore, and the high abundance of gastropods which tolerate freshwater, such as

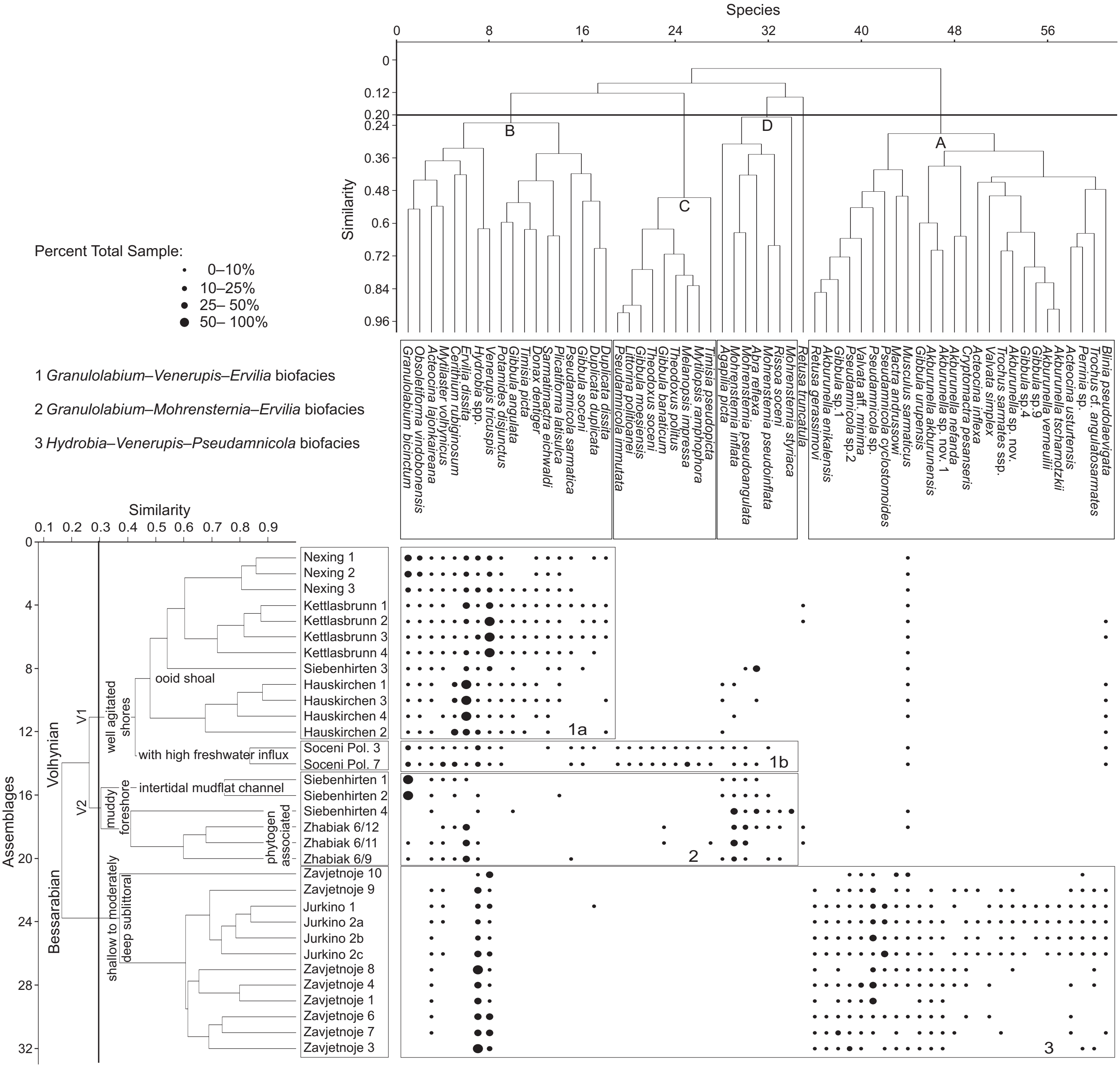

Fig. 13. Q- and R-mode cluster analysis using the Bray-Curtis similarity index. Size of dots indicates relative abundance in samples. Resulting biofacies in combination with Q-mode and R-mode clusters are used to interpret three palaeoenvironments.

Melanopsis impressa, *Theodoxus*, and *Hydrobia*, suggest considerable freshwater influx. This fits well with Jekelius description (1944). He defined the deposits of Soceni Politioanã as a typical intertidal shore, except for the topmost layer, which bears mainly freshwater elements.

Species of the *Granulolabium–Mohrensternia–Ervilia* biofacies are most abundant within all samples from Zhabiak (western Ukraine) and the samples Siebenhirten 1, 2, and 4 (Vienna Basin), which build a cluster within the Q-mode analysis (V2). Thus, we interpret the environment of Zhabiak and Siebenhirten 1, 2, and 4 (Q-mode cluster V2) as a phytal-associated muddy foreshore. The tempestitic shell beds of Zhabiak show highest abundances of the gastropod *Mohrensternia inflata* and the bivalve *Ervilia dissita*. Both species make up 80 % of the total mollusc assemblage. In sample Siebenhirten 4, the rissooids *Mohrensternia inflata* and *M. styriaca* take over, accompanied by *Abra reflexa*. *Mohrensternia* is generally most common in calm pelitic facies (Kowalke and Harzhauser 2004). Typically, the accompanying fauna of *Mohrensternia* changes from gastropods such as *Granulolabium bicinctum* towards a bivalve-dominated fauna with high numbers of *Abra reflexa* and rare *Ervilia dissita* (Harzhauser and

Table 4. Anosim of localities. R-values (A), p-values (B).

A

R-values	Zavjetnoje	Jurkino	Nexing	Hauskirchen	Kettlasbrunn	Siebenhirten	Zhabiak
Zavjetnoje							
Jurkino	0.1838						
Nexing	0.9382	1					
Hauskirchen	1	1	1				
Kettlasbrunn	0.9559	1	1	1			
Siebenhirten	0.9945	0.9792	0.2593	0.7188	0.7396		
Zhabiak	1	1	1	1	1	0.2936	
Soceni	1	1	1	1	1	0.1429	1

B

p-values	Zavjetnoje	Jurkino	Nexing	Hauskirchen	Kettlasbrunn	Siebenhirten	Zhabiak
Zavjetnoje							
Jurkino	0.1674						
Nexing	0.0053	0.0283					
Hauskirchen	0.0024	0.0284	0.0274				
Kettlasbrunn	0.0019	0.029	0.0266	0.0281			
Siebenhirten	0.0017	0.0267	0.1409	0.0261	0.0283		
Zhabiak	0.0084	0.0267	0.1028	0.0316	0.025	0.1182	
Soceni	0.0226	0.0666	0.1012	0.0682	0.0657	0.2631	0.3284

Kowalke 2004). The gastropod genus *Mohrensternia*, restricted to the lowermost Sarmatian, seems to have preferred aberrant salinity conditions: this genus flourished in hypersaline coastal environments and was rare during all normal marine stages in both the Central and Eastern Paratethys (Kowalke and Harzhauser 2004). Samples Siebenhirten 1 and 2 are taken from a sandy channel structure. They are dominated by the gastropod *Granulolabium bicinctum*, which is an indicator for mudflat environments (Harzhauser and Kowalke 2002). Harzhauser and Piller (2004a) correlated this fauna to nearshore conditions based on observations of modern relatives, which are frequently found in littoral settings such as mudflats (Harzhauser and Piller 2004a). As the rissoid gastropods (e.g., *Mohrensternia*) are micro-algal grazers, a phytal cover can be postulated as well (Bandel and Kowalke 1999; Kowalke and Harzhauser 2004).

Species of the *Hydrobia–Venerupis–Pseudamnicola* biofacies are abundant within Bessarabian samples from Jurkino and Zavjetnoje (Q-mode cluster A) from the sandy, shallow to moderately-deep sublittoral. While some of the species in this cluster are restricted to Bessarabian age (*Blinia pseudolaevigata*, *Pseudamnicola cyclostomoides*, *Akburunella nefanda*, *A. verneuilii*, *Acteocina usturtensis*, *A. inflexa*, and *Retusa gerassimovi*) some also occur in Volhynian deposits (*Gibbula urupensis*, *Trochus angulatosarmates*, *Tr. sarmates*, *Akburunella akburunensis*, *Mactra andrussowi*, and *Cryptomactra pesanseris*) (Kolesnikov 1935; Harzhauser and Kowalke 2004). A warm and carbonate-dominated system persisted into the subsequent Bessarabian stage in the Eastern Paratethys. Microbialitic bryozoan-polychaete bioherms flourished in the coastal waters. This semi-closed sea was interpreted as warm, shallow, well-aerated and eutrophic (Goncharova and Rostovtseva 2009). Typical molluscs associated with the carbonate bodies are *Venerupis tricuspis* and various species of *Akburunella*, *Gibbula*, *Acteocina*, and *Pseudamnicola*. The nassariid genus *Akburunella* occurs in the Lower Sarmatian of the entire Paratethys but attained an exceptional diversity during the Bessarabian of the Eastern Paratethys (Harzhauser and Kowalke 2004). At Jurkino and Zavjetnoje, with 5 to 8 different species of *Akburunella*, *A. akburunensis* is the most dominant species. Coastal assemblages, as documented from Zavjetnoje, are dominated by hydrobiids (*Hydrobia* and *Pseudamnicola*). Sample Zavjetnoje 10, which is somewhat isolated in the Q-mode cluster analysis, is strongly dominated by bivalves (*Venerupis tricuspis*, *Musculus sarmaticus*, *Mactra andrussowi*). The stratigraphically valuable *Cryptomactra*, however, is of subordinate importance in the studied samples.

Conclusions

Molluscan abundances of eight Sarmatian localities from the Central and Eastern Paratethys were compared, showing the potential of quantitative comparisons of mollusc faunas in almost isolated systems yielding endemic faunas. Stratigraphic and regional signals are present in these assemblages and are sometimes difficult to disentangle. Samples from Jurkino and Zavjetnoje are of Bessarabian age and come from the Crimean region and are therefore temporally and spatially strongly separated from all other samples. Among the Volhynian localities, samples cluster roughly according to biozones (*Mohrensternia* Zone versus Upper *Ervilia* Zone), but also reflect the different depositional environments of the studied localities. Biofacies show strong palaeoenvironmental affiliations and

Table 5. Anosim of regions. R-values (A), p-values (B).

A

R-values	Vienna Basin	Western Ukraine	Romania
Vienna Basin	–		
Western Ukraine	0.4169	–	
Romania	0.1969	1	–
Crimea	0.8125	1	1

B

p-values	Vienna Basin	Western Ukraine	Romania
Vienna Basin	–		
Western Ukraine	0.0314	–	
Romania	0.2239	0.1	–
Crimea	0.01	0.0027	0.0101

Table 6. Anosim of stratigraphic intervals. R-values (A), p-values (B).

A

R-values	Upper *Ervilia* Zone	*Mohrensternia* Zone
Upper *Ervilia* Zone	–	
Mohrensternia Zone	0.55	–
Bessarabian	0.9894	0.9849

B

p-values	*Mohrensternia* Zone	Upper *Ervilia* Zone
Mohrensternia Zone	–	
Upper *Ervilia* Zone	0.01	–
Bessarabian	0.01	0.01

cover a wide range of possible compositions of Sarmatian nearshore and shallow-water assemblages. The *Granulolabium–Venerupis–Ervilia* biofacies characterises ooid shoals in the Vienna Basin and a well-agitated shore with high freshwater influx in Romania. The *Granulolabium–Mohrensternia–Ervilia* biofacies represents intertidal mudflats in the Vienna Basin and a muddy foreshore with phytal cover in the western Ukraine. The *Hydrobia–Venerupis–Pseudamnicola* biofacies indicates shallow to moderately deep sublittoral settings in Crimea (Ukraine).

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