

Benthic mass-mortality events on a Middle Miocene incised-valley tidal-flat (North Alpine Foredeep Basin)

Oleg Mandic · Mathias Harzhauser · Reinhard Roetzel · Paul Tibuleac

Received: 28 January 2008 / Accepted: 7 April 2008
© Springer-Verlag 2008

Abstract A sedimentological and palaeontological description of the Middle Miocene marine tidal-flat deposits in a ca. 50-km-long incised valley in the eastern part of the North Alpine Foreland Basin is presented. The investigated outcrop documents the environmental shifts in the middle part of this extremely long, narrow, and shallow embayment of the Central Paratethys Sea during the Sarmatian. Sedimentological features point to some tidal influence at that time. The section yields an outstanding Fossilagerstätte with census assemblages of solenid bivalves and potentially pagurized batillariid gastropods in death position. The position of the fossils and the adjoining concretions of former iron-sulfide point to hypoxic events as causes for the benthic mass-mortalities. Based on comparison with modern estuaries, eutrophication and subsequent blooms of macro-algae washing ashore might have triggered the hypoxia in the intertidal zone. The position of the obliquely buried batillariid gastropod shells hints at the occurrence of otherwise completely unrecorded hermit

crabs in the highly endemic fauna of the Paratethys Sea during the Sarmatian.

Keywords Sarmatian · Estuary · Green-tide · Hypoxia · Molluscs · Hermit crabs · Solenid bivalves

Introduction

Incised-valley systems have received much scientific attention over the last two decades since their recognition as potentially important oil reservoirs. Those longitudinal structures, bearing siliciclastic sediment infill, are typically associated with a rapid sea-level fall. According to the definition by Dalrymple et al. (1994, p. 6), an incised-valley always comprises: “(1) an erosional valley, which is formed by river action during a relative sea-level fall; and (2) the valley fill, which may begin to accumulate near the end of the lowstand, but which typically contains sediments deposited during the succeeding base-level rise.” Incised-valley systems are drowned fluvial valleys, and most recent estuaries belong to this geomorphological and environmental category. Classical examples are the Gironde estuary (NW France) or the Chesapeake Bay (eastern USA). The major sea-level fall resulting in incisement of these modern structures was during the Late Pleistocene when the global sea level was about 100 m lower than it is today (Perillo 1995). A similar sea-level fall event occurred within the Middle Miocene during the Serravallian and affected the ancient shelf areas around the globe (Haq et al. 1988).

In the European Central Paratethys Sea, this 3rd-order sequence boundary (Ser 3 of Hardenbol et al. 1998) resulted not only in incisement of numerous fluvial valley systems along its margins (Baráth and Kovác 2000; Strauss et al. 2006) but also caused a major faunal turnover

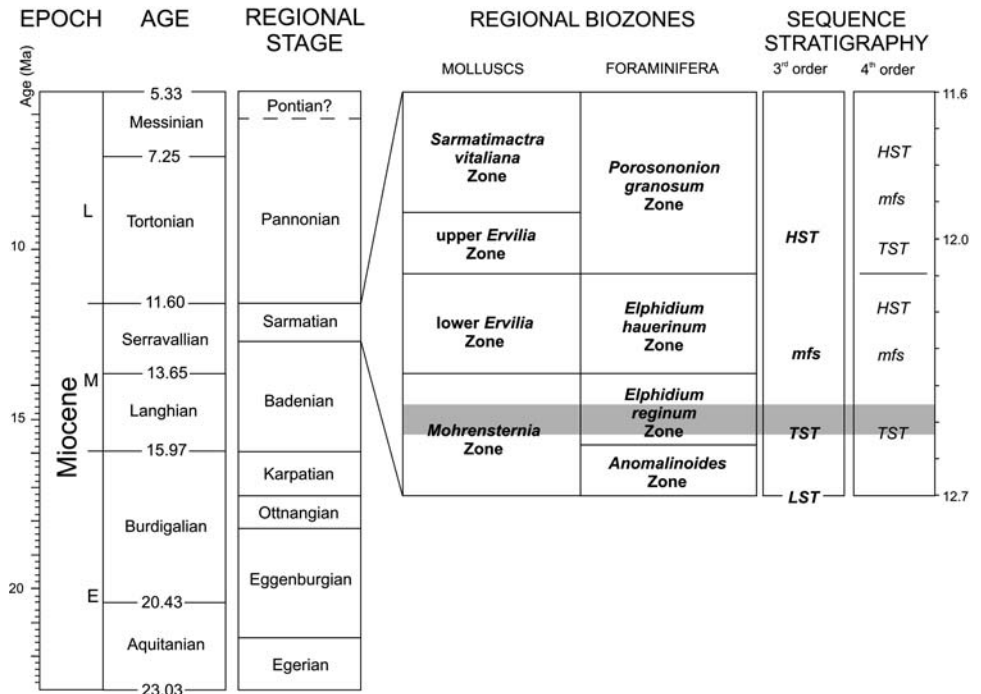
O. Mandic (✉) · M. Harzhauser
Geological-Paleontological Department,
Museum of Natural History Vienna,
Burgring 7, 1010 Vienna, Austria
e-mail: oleg.mandic@nhm-wien.ac.at

M. Harzhauser
e-mail: mathias.harzhauser@nhm-wien.ac.at

R. Roetzel
Department of Sedimentology, Geological Survey of Austria,
Neulinggasse 38, 1030 Vienna, Austria
e-mail: reinhard.roetzel@geologie.ac.at

P. Tibuleac
Faculty of Geography and Geology, Al. I. Cuza University,
B-dul Copou 20A, 6600 Iasi, Romania
e-mail: paul.tibuleac@uaic.ro

Fig. 1 Stratigraphic position of the studied Lower Sarmatian sediments (*gray shading*). The table shows the correlation of standard geochronology and Central Paratethys stages, the regional biozones and the sequence stratigraphic scheme (modified after Harzhauser and Piller 2007; Piller and Harzhauser 2005)



(Harzhauser and Piller 2004a, b, 2007; Piller and Harzhauser 2005; Piller et al. 2007). In the regional stage system, this event coincides with the boundary between the regional stages Badenian and Sarmatian (Fig. 1). A major Central Paratethyan extinction event took place, which was subsequently compensated by a conspicuous endemic evolution of the surviving taxa (Harzhauser and Piller 2007). Up to now, no data exist on the recovery phase of the benthic intertidal faunas after the extinction event. The present study describes such a rare autochthonous Early Sarmatian post-extinction fauna and characterizes the depositional environments in an incised valley striking about 50 km from the Vienna Basin westward into the Eastern Alpine Foredeep. The significance of in situ occurrence of several mollusc taxa in terms of palaeoenvironmental interpretation will be discussed in detail.

Geological setting and outcrop description

The last deep marine sediments were deposited in the eastern part of the North Alpine Foreland Basin during the Early Badenian (~Langhian; ca. 15 Ma; Fig. 1) when an active fluvial system already loaded Alpine debris into the foredeep from the southwest (Harzhauser et al. 2003). During the Middle to Late Badenian (~Late Langhian–Early Serravallian) the foreland basin emerged and a large river found its way via a transversal tectonic structure of the Zaya river valley. This palaeo-Zaya river transported conspicuous amounts of debris into the northwestern Vienna Basin, forming huge deltaic bodies (Jiriček and Seifert

1990). A lowstand at the end of the Badenian resulted in further incisement of that palaeo-Zaya river and a basinward progradation of the deltas (Strauss et al. 2006). During the subsequent Early Sarmatian transgression at ca. 12.5 Ma, this new geomorphologic structure became flooded again for about 0.2 Ma (Fig. 1). At the same time, the rise of the relative sea level allowed the Central Paratethys Sea to reach about 50 km into the river valley. The described sediments are part of this system and represent roughly the central part of the marine embayment. They cropped out along the road from Hollabrunn to Aspersdorf (48°34'23"N; 16°05'09"E, Lower Austria) (Fig. 2). During a field campaign of the Institute of Paleontology, University of Vienna, in July 1994, a small pit was excavated by a caterpillar along a total length of about 14 m (Figs. 3, 4, 5).

The locality Hollabrunn/Aspersdorf or sandpit Weik has experienced a long history of investigation starting with Suess (1866), Bittner (1883), and Veters (1914). The first thorough palaeontological study dates back to Papp (1948, 1950, 1956), who focused on the marine mollusc fauna, whereas Schütt (1967) reported on the diverse terrestrial gastropod assemblage. Later, Papp and Steininger (1974) introduced the section as a faciostratotype (i.e., auxiliary stratotype of different facies) of the Lower Sarmatian. Finally, Kowalke and Harzhauser (2004) referred to the section Hollabrunn/Aspersdorf when describing the rissoid fauna of the Central Paratethys. During recent geological mapping, Roetzel (2003, 2007a) showed that these deposits are part of a ca. 50-km-long continuous Sarmatian sedimentary belt following a roughly WSW–ENE trending narrow belt from the Bohemian Massif in the west to the Vienna Basin in the east.

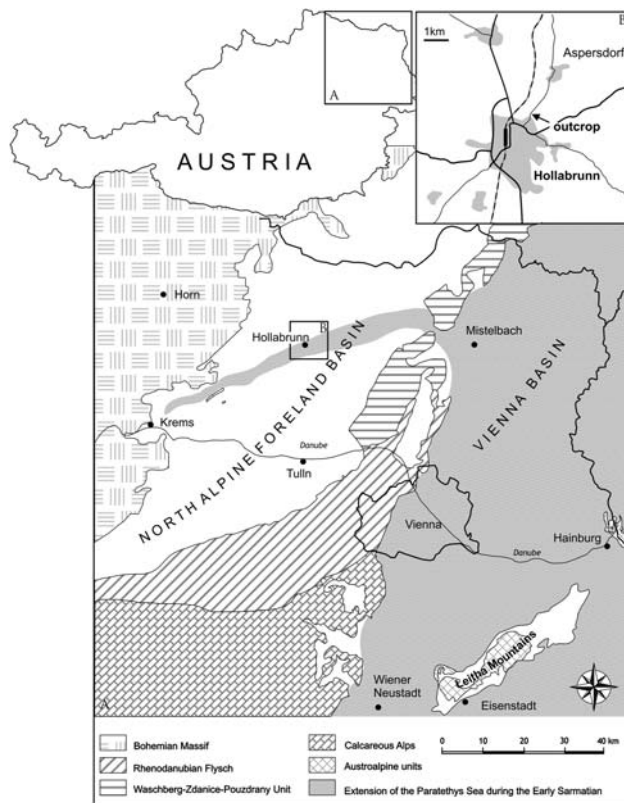


Fig. 2 Geographic and regional geological setting (**a**) of the studied outcrop (**b**), modified after Mandić et al. (2002) and Austrian topographic map 1:50 000 (ÖK 50, sheets 22 Hollabrunn and 23 Hadres). The wave-signature indicates the extension of the Paratethys Sea into the North Alpine Foreland Basin based on mapping results of Fuchs et al. (1984); Grill (1968); Roetzel (1998, 2003, 2007a, b)

Description

The Hollabrunn/Aspersdorf section comprises an about 4-m-thick succession of seven lithological units (Figs. 3, 4, 5). The lower six are characterized by interbeddings of sand, pelites and gravel, whereas the topmost gravel bed represents Pleistocene fluvial gravel.

Unit 1 (bed 1; 50 cm; gravel and sand with terrestrial gastropods): the exposed succession starts with a fine to medium gravel bed (bed 1a) passing upwards into gravel-bearing sands (bed 1b). The polymict gravel components are well rounded, consisting of quartz, limestone, sandstone and crystalline lithoclasts. Mud clasts are present as well. Lithoclasts and mud clasts maximally attain 7 cm in diameter. Towards the top the gravel is intercalated in poorly sorted, silty, medium to fine sand.

Fragmented mollusc shells and various terrestrial gastropods such as *Cepaea gottsckicki* Wenz 1919; and *Tropidomphalus gigas* Papp 1951 frequently occur. Reworked Early or Middle Miocene oyster shells occur sporadically, characterized by heavily abraded surfaces. Borings by *Litho-*

ophaga within these shells point to a pre-Sarmatian age, because the boring bivalve *Lithophaga* became extinct in the Paratethys at the end of the Middle Miocene Badenian stage (Kojumdgieva 1960; Nevešská et al. 1993; Schultz 2001).

Unit 2 (bed 2; 45 cm; sand with mixed terrestrial and aquatic-marine molluscs): a single gravelly layer (bed 2b) is intercalated in predominantly fine sand. In the basal fine sandy bed (bed 2a), silty layers are interbedded, commonly showing convolute bedding. The above following, max. 10-cm-thick, polymict, gravelly intercalation contains rounded to subangular components up to 2 cm in diameter. In the fine sand above (bed 2c), small, flat current ripples occur.

The basal bed (bed 2a) still comprises well-preserved terrestrial gastropods, along with poorly preserved *Granulolabium*. With the gravelly intercalation (bed 2b) aquatic molluscs become frequent. Among the gastropods, *Granulolabium bicinctum* (Brocchi 1814), and *Turritella eryna sarmatica* Papp 1954 are common, whereas *Obsoletiforma vindobonensis* (Laskarev 1903), *Plicatiforma pseudoplicata* (Friedberg 1934), and *Solen subfragilis* Eichwald 1853 represent the predominating bivalves. Molluscs are commonly fragmented and with abraded surfaces, especially within the gravel horizon. Above (bed 2c), well-preserved *Granulolabium* tests also occur. Bivalve shells are disarticulated and no indication for life/death positions is present throughout the unit.

Unit 3 (bed 3; 65 cm; sand and pelitic sediments with ripple- and convolute bedding, poor in fossils): above a well-defined, wavy-shaped erosional surface, the unit starts with silty-clayey sediments (bed 3a), passing upward into fine sand to fine sandy silt (bed 3b). Original inter-bedding is almost completely destroyed by intensive convolute bedding (Fig. 5d). Above, inter-bedding of fine sands with silty fine sands (bed 3c) shows intensive ripple bedding with asymmetrical current ripples. Convolute bedding is rare. To the northeast, bed 3c wedges out toward a relief of the underlying bed 3b (Fig. 3).

The fossils, mainly *Granulolabium bicinctum* shells, are concentrated at the boundary with Unit 2. The rest of the unit is, except for scattered mollusc fragments and fossil wood remains, barren of fossils.

Unit 4 (beds 4–7; 110 cm; sand and pelitic sediments with burrows of *Solen subfragilis*): this unit is characterized by 10 to 20-cm-thick fine to medium sands interbedding with silty to clayey sediments. It overlays an erosional boundary. In its lower part, the sands include scattered mud clasts and pebbles (bed 4a). The unit is bioturbated (Fig. 5e). From interbedded pelitic layers (beds 4b, 4c, 5, 7a, 7c), burrows of *Solen subfragilis* extend downwards into the sands below. Ripple bedding with wave ripples sometimes occur in the upper part of this unit (bed 7b).

Burrows, filled with sand or silt, associated with in situ *Solen subfragilis* are typical, along with well-preserved

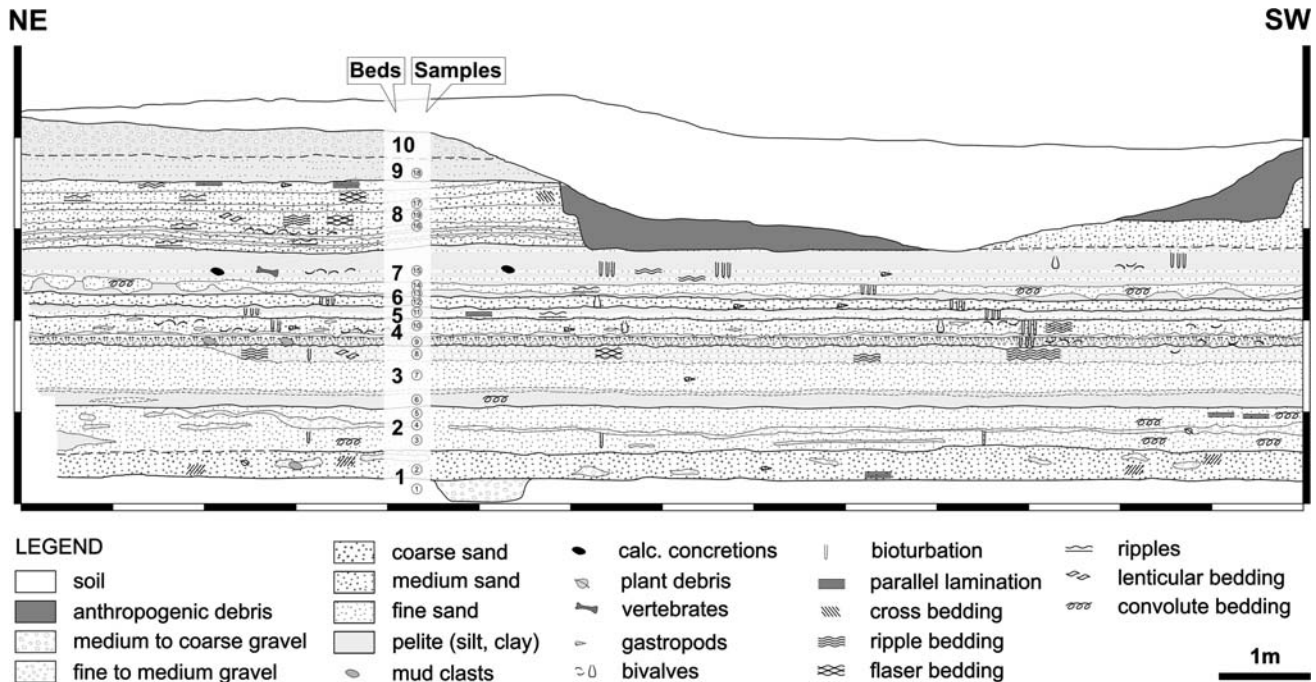


Fig. 3 Detailed sketch of a 14-m-long section of the Hollabrunn/Aspersdorf outcrop showing predominantly *horizontal* bedding planes

tests of *Granulolabium bicinctum*. The latter frequently show a limonitic concretion around the aperture and typically lie in conspicuous aperture-up position. A diverse mollusc fauna of *Obsoletiforma vindobonensis* (Laskarev 1903), *Abra reflexa* (Eichwald 1830), *Sarmatimactra eichwaldi* (Laskarev 1914), *Ervilia dissita* (Eichwald 1830), *Turritella eryna sarmatica* Papp 1954, *Ocenebra striata* (Eichwald 1830), *Acteocina lajonkairieana* (Basterot 1825), and *Euspira helicina* (Brocchi 1814) is documented. Small-sized hydrobiids and various species of *Mohrensternia* are most abundant in this unit. All bivalves were found articulated and in life position, characterized additionally by limonitic concretions within and around the shell. The species diversity is greatest within bed 4.

Unit 5 (bed 8; 70 cm; ripple bedded sand with mollusc debris, Fig. 5c): The unit contains 5 to 10-cm-thick layers of fine to medium sands that always show ripple cross bedding of current ripples, mostly with form sets on top of it. In rare cases, climbing-ripple lamination is observable. Between these ripple bedded sands, a few cm-thick intercalations of silty fine sands occur, covering and level out the relief of the form sets. The topmost sands of the unit show upper plane bed horizontal lamination (bed 8i).

Shells and fragments of *Sarmatimactra eichwaldi*, *Solen subfragilis*, *Obsoletiforma vindobonensis*, *Granulolabium bicinctum* and *Mohrensternia* spp. form stringers or appear as accumulations in the ripple bedded sands, mostly in ripple troughs. In situ occurrences are absent, except for the boundary region with Unit 6. There, large *Granulolabium* partly occur in aperture-up

position and exhibit a limonitic concretion around the aperture.

Unit 6 (bed 9; 25 cm; pelitic sediment with large bati-lariid gastropods): in the uppermost part of the Sarmatian sediments, massive, micaceous, fine sandy and clayey silts yield scattered *Granulolabium bicinctum*.

Unit 7 (bed 10; max. 50 cm; Pleistocene gravel formed by reworked Upper Miocene (Pannonian) gravel): an erosive surface is overlain by well-rounded gravel in a silty to sandy matrix, passing upwards into the soil horizon. The gravel is reworked from the Pannonian fluvial Hollabrunn-Mistelbach Formation and belongs to a Pleistocene terrace of the Göllersbach River (Roetzel 2003).

Biostratigraphy

Aside from the index genus *Mohrensternia*, the occurrence of *Abra reflexa*, *Plicatiforma pseudoplicata* and *Turritella eryna sarmatica* allow a dating of the succession as Early Sarmatian *Mohrensternia* Zone (see biostratigraphic scheme of Harzhauser and Piller 2004b). Furthermore, the foraminifer assemblage with large-sized elphidiids allows a correlation of the section with the *Elphidium reginum* zone defining the upper part of the *Mohrensternia* Zone (Fig. 1).

Granulometric analysis

Granulometric analyses were conducted on 19 samples to characterize the sediments and to analyze the depositional

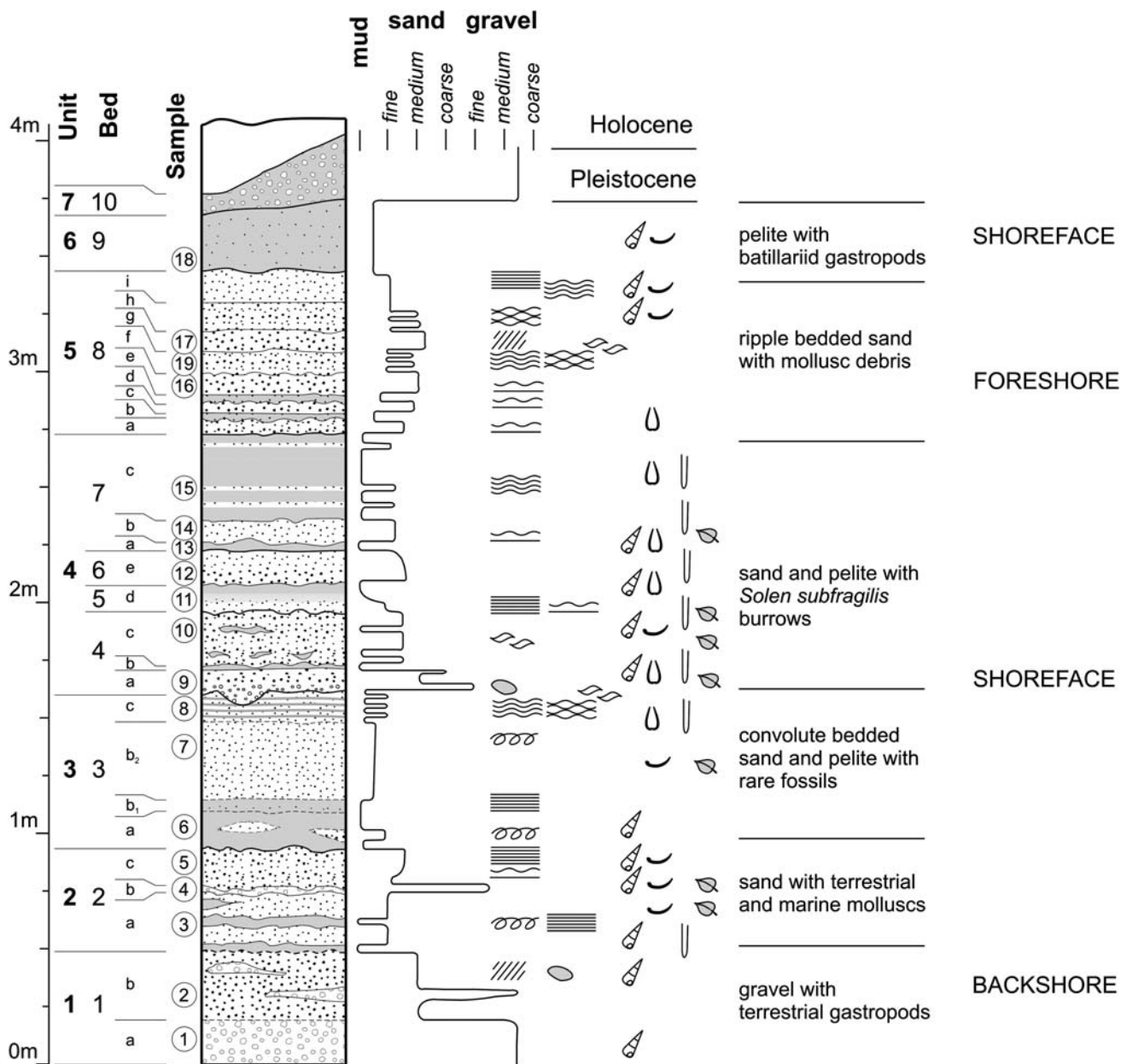


Fig. 4 Log of the Hollabrunn/Aspersdorf section indicating sedimentological characters and fossil distribution (see Fig. 3 for legend)

environment. Granulometric data of weight percents for gravel, sand, silt and clay as well as means (first moment), standard deviations (sorting, second moment) and skewness (third moment) are presented in Table 1. The grain size distribution in phi values of all samples, presented in log-probability plots, is shown in Fig. 6 (see Figs. 3, 4 for position of the samples in the section).

No fining or coarsening upward trend is visible in the section. The whole (about 4-m-thick) succession in the section Hollabrunn/Aspersdorf shows an alternation of layers rich in sand, frequently interrupted by fine-grained layers dominated by silt and clay. Only in the basal Units 1

(samples 1, 2) and 2 (sample 4) are considerable amounts of mostly fine-grained gravel present, reflected in mean values of 0.6–2 Phi (Table 1). Most of the sands above in the Units 2–5 (samples 5, 8, 9, 10, 12, 14, 16, 17, 19) are medium to fine sands, sometimes silty, with mean values between 2.7 and 4.1 Phi (Table 1). The better sorting is mirrored by standard deviation values between 1.2 and 2.7 Phi. The skewness of these sands is strongly positive (values between 3 and 7 with a maximum between 4 and 5), indicating the dominance of the coarser grain sizes in these sediments. The intercalated pelitic sediments of Units 2–6 (samples 3, 6, 7, 11, 13, 15, 18) are poorly sorted silts,

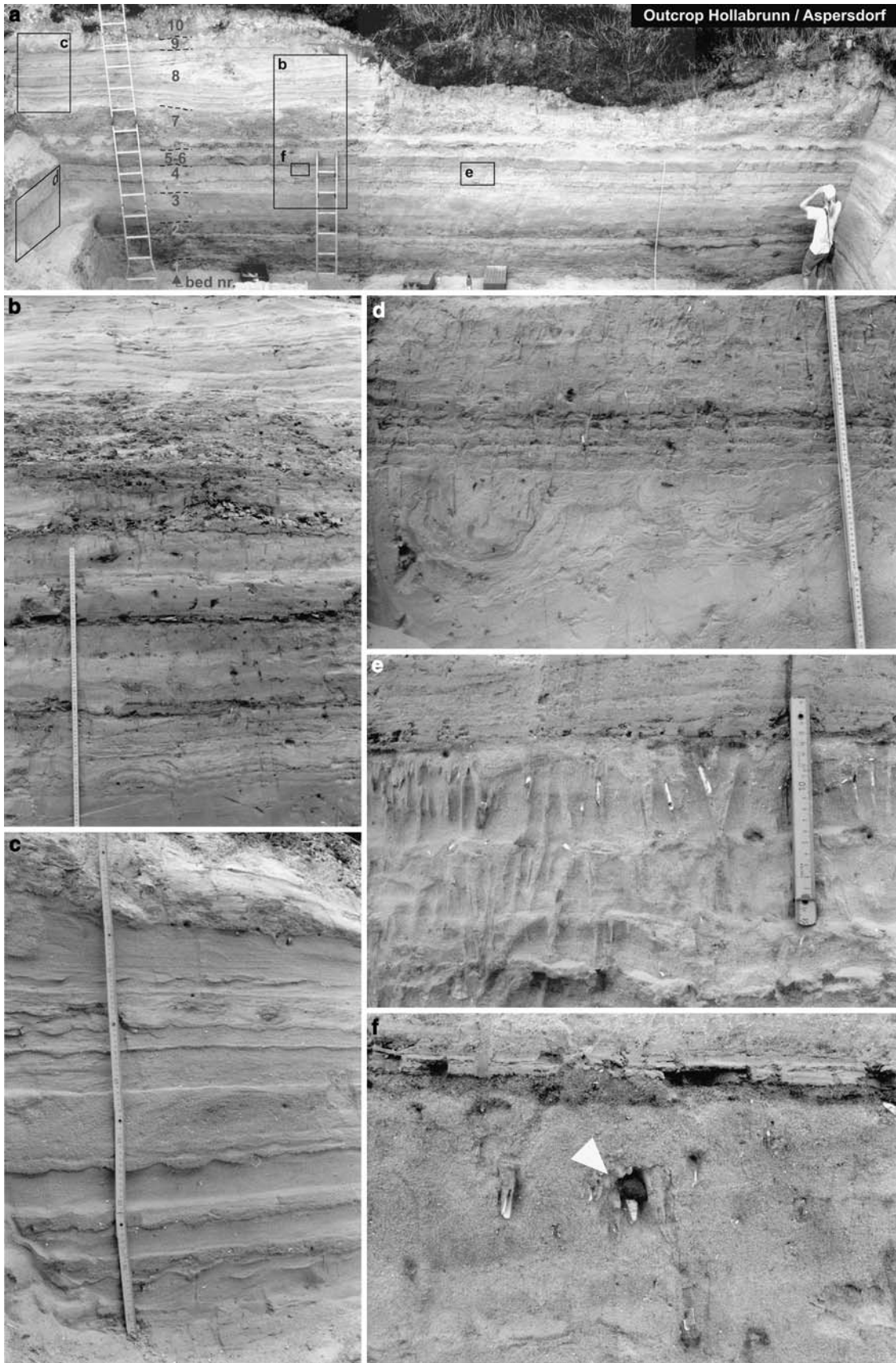


Fig. 5 Sedimentological and taphonomic features of section Hollabrunn/Aspersdorf. **a** Outcrop overview showing the distribution of the lithologic units with beds 1–10 (positions of photographs b–f are additionally marked). **b** Beds 4–8. **c** Bed 8 showing predominant ripple bedding except for its upper part, characterized by parallel bedding. **d** Intensive convolute bedding and water escape structures inside bed 3 followed by horizontally layered interbedding of sands and silts. **e** Intensive bioturbations of bed 4; solenid bivalve burrows are well preserved, densely distributed and mostly still showing the producer. **f** *Granulolabium* shells in upside down position with aperture covered by limonite concretions (arrow)

clayey-sandy silts, clayey sandsilts, clayey silts, claysilts and siltclays with mean values of 7–10.6 Phi. The skewness of these pelites is slightly positive to nearly symmetric, with values between 0 and 1.4 (Table 1).

The negative correlation between sorting and skewness and the partitioning of sands and pelitic sediments in two distinct areas is clearly expressed in the plot (Fig. 6). The grain size distribution in Phi values, presented in log-probability plots (Fig. 6), usually shows distinctly separated log-normal populations attributable to transport by rolling, saltation and suspension. In the basal gravelly samples 1, 2, 4, the relatively high amount of the rolling fraction (20–30%) is not very well separated from the saltation population. The suspension population, however, is always clearly disconnected from the saltation fraction by an obvious break; it sometimes exceeds 25% (sample 4).

The sands (samples 5, 8, 9, 10, 12, 14, 16, 17, 19) generally have clearly separated log-normal populations. Signifi-

cant is a very small rolling population with a low slope, indicating poor sorting, breaking at 0.5–1.25 Phi. The well-sorted, high-slope saltation population predominates with 89–97% and only rarely displays an internal break (sample 8). The fine truncation point consistently lies between 3.75 and 4.25 Phi. The mostly small, low-slope, moderately sorted suspension population again is separated against the saltation population by a clear break at 3.75–4.25 Phi.

This type of grain size distribution is similar in shape to those described from channel sands from estuaries and tidal areas (Glaister and Nelson 1974; Sindowski 1957; Visher 1969). Visher (1969) and Visher and Howard (1974) describe comparable grain size distributions with three well-defined populations of this type from the Altamaha river estuary, and Sindowski (1957) found such distributions in tidal sands of the East Frisian coast.

The intercalated pelitic sediments (samples 3, 6, 7, 11, 13, 15, 18) show obviously different grain size distributions. Like the sands, they have an insignificant traction load but, contrary to the sands, more widely scattered coarse truncation points between 1.75 and 3.25 Phi. The lesser-sorted saltation population is very often divided by internal breaks into sub-populations probably reflecting reworking by burrowing organisms (Visher 1969, fig. 21b). The saltation segment is 40–63% of the whole size plot. The junction of saltation and suspension segments is also widely scattered between 4.25 and 8.25 Phi; moreover, it is gradational rather than sharply delineated. The portion of suspension is always high (37–60% of the whole size plot) and low slope moderately sorted.

Table 1 Granulometric data from samples of the studied section Hollabrunn/Aspersdorf

Sample	Nomenclature	Gravel (%)	Sand (%)	Silt (%)	Clay (%)	Mean (phi)	Stdev (phi)	Skewn
HL-G-01	graveIsland	34.37	58.35	4.06	3.22	0.58	3.36	2.25
HL-G-02	Sand	6.71	88.03	3.29	1.97	1.93	2.58	3.64
HL-G-03	Clayey-sandy silt	0.00	15.28	61.96	22.76	7.45	4.25	1.22
HL-G-04	Silty-gravelly sand	22.46	59.15	9.55	8.84	2.04	5.13	1.84
HL-G-05	Sand	0.08	89.09	8.81	2.02	3.11	2.01	4.66
HL-G-06	Siltclay	0.73	5.95	42.19	51.13	10.38	4.60	0.02
HL-G-07	Clayey-sand silt	0.00	22.06	56.92	21.02	6.99	4.25	1.36
HL-G-08	Silty sand	0.00	82.04	13.57	4.39	4.08	2.63	4.10
HL-G-09	Sand	0.35	94.69	4.45	0.51	2.67	1.17	2.96
HL-G-10	Sand	0.07	90.91	6.25	2.77	3.32	2.05	4.51
HL-G-11	Clayey silt	0.00	6.84	68.72	24.45	8.07	4.87	1.23
HL-G-12	Sand	0.01	93.12	4.34	2.53	3.14	2.01	4.73
HL-G-13	Siltclay	0.21	6.02	45.26	48.51	10.63	4.99	0.25
HL-G-14	Sand	0.04	91.68	5.02	3.26	3.50	2.46	4.79
HL-G-15	Clayey silt	0.10	3.75	53.26	42.89	9.53	4.34	0.37
HL-G-16	Sand	0.14	96.74	2.31	0.81	2.74	1.19	4.91
HL-G-17	Sand	0.12	97.09	1.59	1.21	2.68	1.64	6.98
HL-G-18	Clayey sandsilt	0.00	27.84	49.97	22.19	7.24	5.00	1.34
HL-G-19	Silty sand	0.15	79.28	15.26	5.31	4.10	2.72	3.46

Nomenclature after Füchtbauer (1959) and Müller (1961); proportions of gravel, sand, silt and clay in weight percent; mean: first moment in Phi, standard deviation (Stdev): second moment in Phi; skewness (Skewn): third moment
For position of the samples in the section see Figs. 3, 4

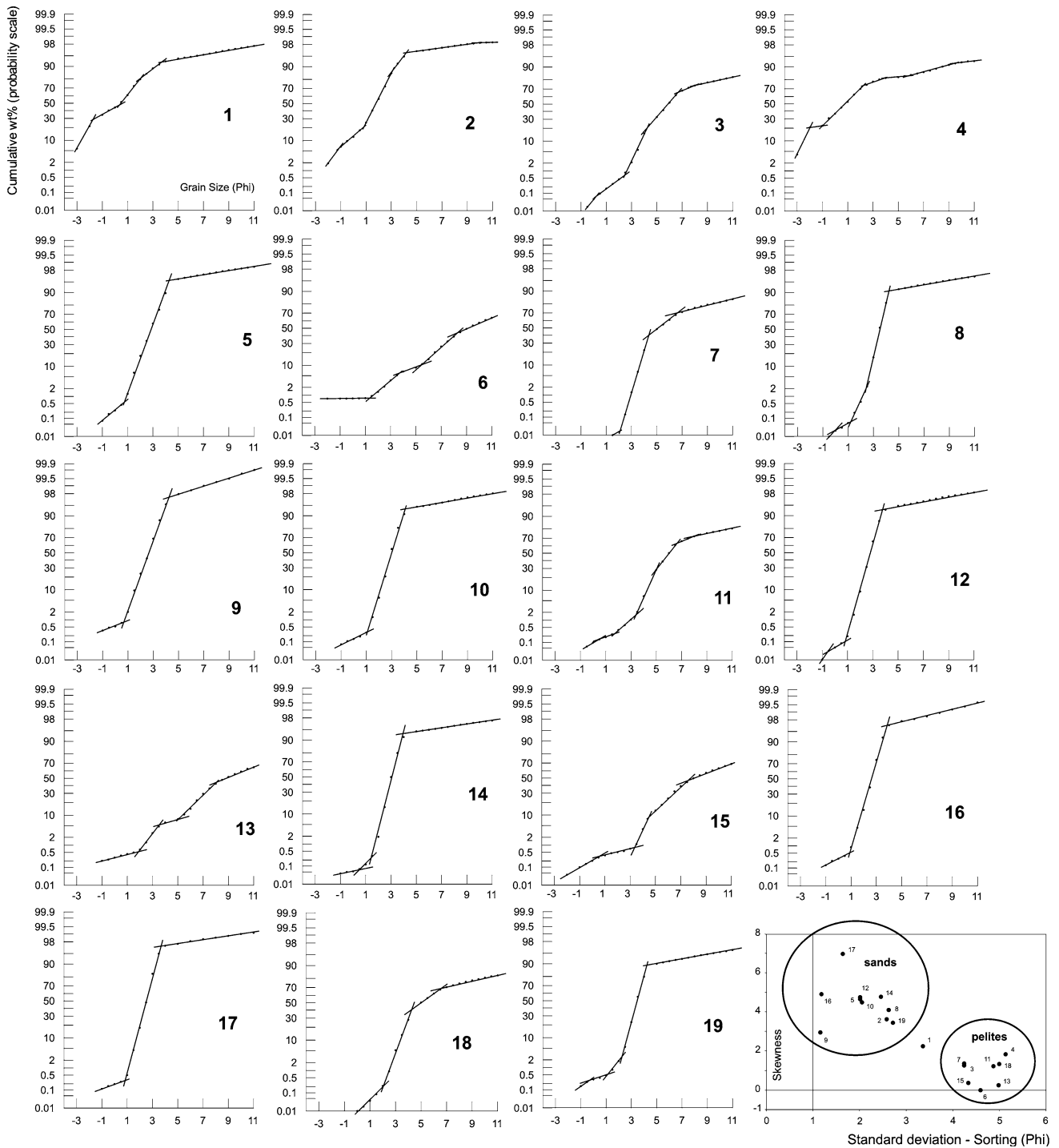


Fig. 6 Grain size distribution in log-probability plots from samples of the section Hollabrunn/Aspersdorf and relation of standard deviation (second moment) vs. skewness (third moment) of these samples. The numbers 1–19 correspond with sample numbers

Palaeoecology

The collected fauna comprises aquatic-marine as well as abundant terrestrial elements (Table 2; Fig. 7). The aquatic elements—predominantly bivalves—display in situ occur-

rences, which are often associated with preserved burrows. Thus, at least within units with preserved burrows, the articulated bivalves are clearly within-habitat elements. Based on their ecological requirements, the assemblage points to a shallow subtidal to lower intertidal depositional

Table 2 List of molluscs collected at the studied section

Gastropoda		
Neritoidea	Neritidae	<i>Agapilia cf. picta</i> (Ferussac 1825)
Cerithioidea	Turritellidae	<i>Turritella eryna sarmatica</i> (Papp 1954)
	Potamididae	<i>Granulolabium bicinctum</i> (Brocchi 1814)
Rissoidea	Rissoidea	<i>Mohrensternia angulata</i> (Eichwald 1853)
		<i>Mohrensternia hollabrunnensis</i> Kowalke and Harzhauser (2004)
		<i>Mohrensternia hydroboides</i> (Hilber 1897)
		<i>Mohrensternia inflata</i> (Homes 1856)
		<i>Mohrensternia sarmatica</i> Friedberg 1923
		Hydrobiidae
		<i>Hydrobia suturata</i> (Fuchs 1873)
Naticoidea	Naticidae	<i>Euspira helicina</i> (Brocchi 1814)
Muricoidea	Muricidae	<i>Ocenebra striata</i> (Eichwald 1830)
Acteonoidea	Acteocinidae	<i>Acteocina lajonkaireana</i> (Basterot 1825)
Bivalvia		
Cardioidea	Cardiidae	<i>Plicatiforma pseudoplicata</i> (Friedberg 1934)
		<i>Inaequicostata janoscheki</i> (Papp 1954)
		<i>Obsoletiforma vindobonensis</i> (Laskarev 1903)
Mactroidea	Mactridae	<i>Sarmatimactra eichwaldi</i> (Laskarev 1914)
Solenioidea	Solenidae	<i>Solen subfragilis</i> (Eichwald 1853)
Tellinoidea	Semelidae	<i>Abra reflexa</i> (Eichwald 1830)
		<i>Ervilia dissita</i> (Eichwald 1830)

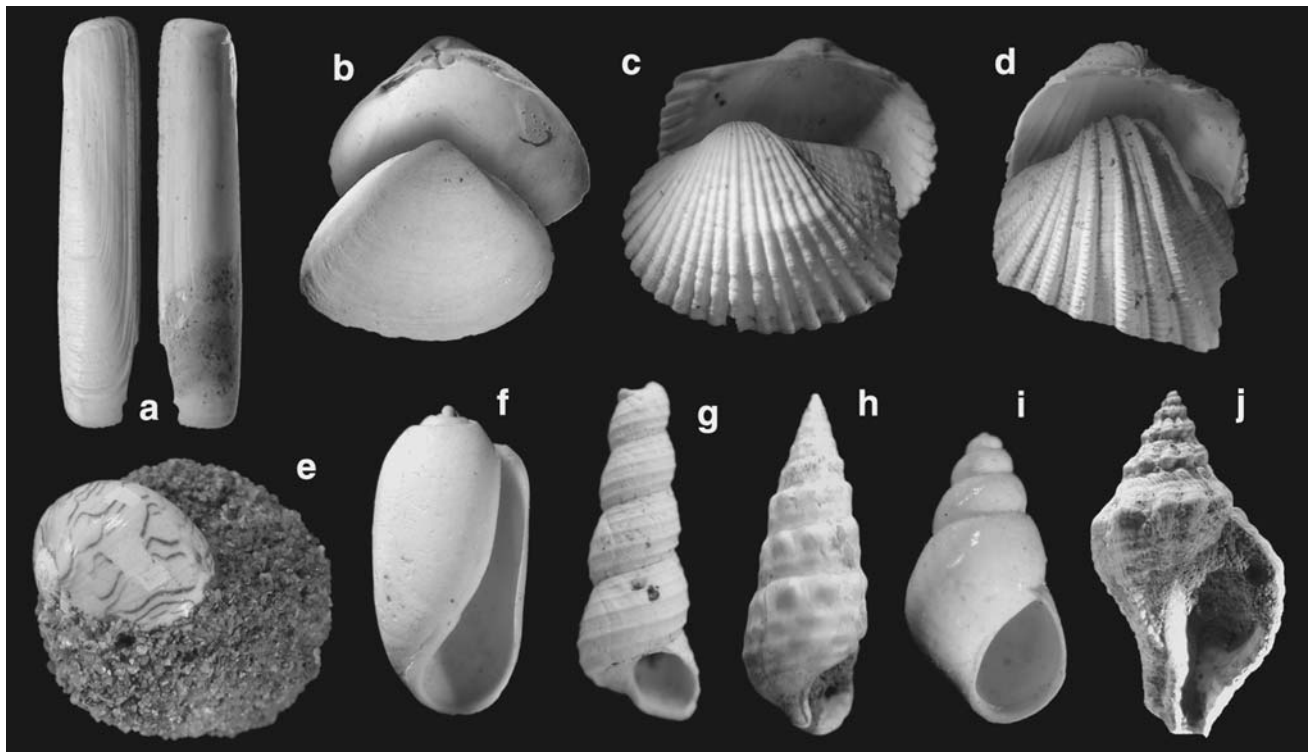


Fig. 7 Characteristic of molluscs in the studied section. **a** *Solen subfragilis* Eichwald 1853, length 28.1 mm—right exterior and right interior view; **b** *Sarmatimactra eichwaldi* (Laskarev 1914), right valve, 13.6-mm length; **c** *Obsoletiforma vindobonensis* (Laskarev 1903), left valve, 9.1-mm length; **d** *Plicatiforma pseudoplicata* (Friedberg 1934), left valve, 9-mm length; **e** Neritid gastropod with limonitic concretion

at aperture, concretion radius 8.5 mm; **f** *Acteocina lajonkaireana* (Basterot 1825), height 2.1 mm; **g** *Turritella eryna sarmatica* (Papp 1954), height 20.5 mm; **h** *Granulolabium bicinctum* (Brocchi 1814), height 22.6 mm; **i** *Hydrobia andrusowi* Hilber 1897, height 1.7 mm; **j** *Ocenebra striata* (Eichwald 1830), height 23.6 mm

environment. In contrast, the terrestrial gastropods are interpreted as exotic elements deriving from a backshore environment, brought in by wind or flows.

Marine assemblage

The marine assemblage represents a very characteristic Early Sarmatian fauna that can be detected throughout the Paratethyan coasts. Its low diversity is counterbalanced by an enormous mass of individuals composed of few predominating species. Among gastropods, only the batillariid *Granulolabium bicinctum* and the several rissoid species (Table 2; Fig. 7) appear in high numbers. *Granulolabium bicinctum* displays a vast range of morphologies, from strongly sculptured to nearly smooth. As its modern congeners, it probably lived in large populations, browsing algae and organic detritus in the littoral zone (Lozouet et al. 2001). Similar habitat preferences might be expected for the ubiquitous hydrobiids. Modern counterparts such as *Hydrobia ulvae* (Pennant 1777) form large populations along the mud flats of the North Sea, inhabiting small ponds and pools during low tide (Hertweck 1990).

Predatory pressure on the mollusc fauna by carnivorous gastropods and decapods seems to have been low during the Early Sarmatian. The carnivorous guild—documented by the presence of *Euspira helicina*, *Ocenebra striata* and *Acteocina lajonkaireana*—is strongly underrepresented compared to the fully marine coastal faunas of the previous Badenian stage. In the studied section, the naticid *Euspira helicina* and the muricid *Ocenebra striata* are rare elements. Conspicuously, traces of naticid predation indicated by boreholes in investigated shells is also infrequent. As already discussed by Harzhauser and Kowalke (2002), predation by crustaceans is hardly documented within the Sarmatian shelly fauna, probably due to an ecologically triggered extinction of large parts of the crab fauna at the Badenian/Sarmatian boundary. Most likely, the very frequent *Acteocina lajonkaireana* preyed on foraminifers, as has been documented for recent species of *Acteocina* and *Cylichna* (Bazas and Carle 1979; Shonman and Nybakken 1978).

The bivalves (Table 2; Fig. 7) are represented by fewer species than the gastropods. Within Unit 4, large numbers of *Solen subfragilis* and scattered *Sarmatimacra eichwaldi* were found in situ, confirming their autochthonous within-habitat presence. All bivalve species except for *Abra reflexa* are suspension-feeding burrowers typical for shallow-water environments (Stanley 1970). The latter species is a deposit-feeding burrower. Its modern relatives inhabit various muddy environments from the shoreface down to the bathyal (Willmann 1989).

The recent solenid bivalves are typical shoreface inhabitants. Despite their rather short siphons, they are deep

burrowers. When filter feeding, they are positioned close to the burrow opening. When disturbed, they quickly burrow down and can even swim for short distances by jet propulsion if excavated (Stanley 1970; Poppe and Goto 1993). The recent *Solen marginatus* (Pennant 1777) prefers sandy and sandy to muddy bottoms from 0.5 to 3 m water depth in the Adriatic Sea (Milišić 1991). Similar to its South African relatives, *Solen capensis* Fischer 1881 and *S. corneus* Lamarck 1818, this species, although principally preferring fully marine settings, is typically distributed close to or within estuaries (Branch and Branch 1981). This reflects their suspension-feeding mode of life, facilitated by the rich nutrient supply through the fluvial influx. Correspondingly, the macrtrids are extremely dominant in such settings. Macrtrid mass occurrences, with densities of up to 400 individuals per m², have been reported by Branch and Branch (1981) especially in parts of estuaries and lagoons exposed to strong currents, like in the channel entering the Langebaan Lagoon of the Atlantic coast of South Africa.

Terrestrial assemblage

Terrestrial gastropods are most frequent in the basal gravelly Unit 1 and may form small lens-like accumulations (Schütt 1967). In contrast, no freshwater gastropods were detected during the excavation, pointing to a very low freshwater influx at this part of the estuary. Such a pattern indicates that most terrestrial shells derive from the adjoining hinterland instead of being transported via a drainage system from the mainland towards the embayment of the Paratethys Sea. The concentration of those remains at the basal unit can best be explained by its backshore position, where the terrestrial influence was potentially the strongest.

Among the 38 terrestrial gastropods described by Schütt (1967), four are predominant: *Pomatias consobrinum*, *Carychium* cf. *sandbergeri*, *Tropidomphalus gigas* and *Cepaea gottschicki*. Based on their abundance and the above-stated limited transportation by rivers, these taxa apparently represent inhabitants of the adjacent terrestrial environments. Indeed, Carychiidae are facies indices for humid lakeside environments (Lueger 1981), although they may also occur in humid foliage (Harbeck 1996). The extant *Pomatias elegans* (Müller 1774), as a potential relative of the common *Pomatias consobrinum*, inhabits open woodland areas and scree (Ložek 1964; Fechter and Falkner 1989). The two helicid species *Tropidomphalus gigas* and *Cepaea gottschicki* are frequently co-occurring species in the Sarmatian and Pannonian, pointing to at least partly overlapping habitat preferences. Lueger (1981) interpreted *Tropidomphalus gigas* as an inhabitant of moderately dry shoreline environments vegetated by shrubs. Moist near-shore habitats would also be settled by *Vertigo* (*Vertilla*) *angulifera* Boettger 1884 and *Vertigo* (*Vertigo*) *callosa*

(Reuss 1849). Moderately moist woodland settings with shrubs and foliage might be indicated by the occurrences of *Discus pleuradus* (Bourguignat 1881) or *Azeca tridentiformis* (Gottschick 1911). Species potentially settling more open and drier habitats, such as *Vallonia subcyclophorella* (Gottschick 1911), *Strobilops costata* (Clessin 1877) or *Truncatellina lentilii* (Miller 1900), although present, are of subordinate importance in the total spectrum.

Thus, the composition of the land snail fauna and the frequency of palaeologically significant taxa suggest only moderately moist, vegetated levees surrounding the inlet of the Paratethys in Early Sarmatian times.

Taphonomy and palaeoenvironment

The section Hollabrunn/Aspersdorf is exceptionally interesting due to the in situ occurrence of several taxa. Among these, the bivalve *Solen subfragilis* and the gastropod *Granulolabium bicinctum* are especially significant in terms of palaeoenvironmental interpretations.

Solen subfragilis taphofacies—victims of hypoxia

The position of numerous *Solen subfragilis* shells corresponds to the life position of the animals (Fig. 5e). The up to 4 cm long, small-sized and elongated solenids thus formed dense populations in the sandy and muddy layers of Unit 4. Most in situ occurrences are confined to the upper part of fine sand beds, overlain by a several-cm-thick pelitic bed. From the sand/mud interface the burrow depths range from zero down to 9–11 cm. Usually the depth of bioturbation is well indicated by a thin tube of limonitic fine sand corresponding to the former burrowing canal of the clam. These tubes are usually associated with articulated shells of *Solen subfragilis*. The population density was measured in two different layers in a 35-cm-long transect. Each layer yielded 4–16 specimens, allowing a maximum population density approximation of up to 2,000 individuals per square metre. This calculation is realistic, as modern solenids such as the Pacific razor clam *Siliqua patula* (Dixon 1789) have average settling densities from 14,900 to 39,665 juvenile specimens per square metre (Tegelberg and Magoon 1969).

The post-mortem position of those bivalves within their burrows is a very conspicuous taphonomic feature. Solenid mass mortality is described from the intertidal areas of the Wadden Sea for the morphologically and ecologically very similar *Ensis directus* (Conrad 1843; Willmann 1989). The mechanism behind those mass mortalities is still poorly understood. The speculations range from plagues by parasites through the influence of cold periods to energy depletion after spawning (Cadee 2000). During those events, occurring typically during the winter season, the solenids

partly leave their burrows (at least half their length above the sediment) and are unable to re-burrow. This makes them easy prey for herring gulls, which crack the shell characteristically, or they are washed ashore by waves and accumulate as lags on the beach (Willmann 1989). At the Hollabrunn/Aspersdorf section, such features are completely absent. The solenids remained in their burrows without becoming exhumed by wave action and without being cracked by predators. In estuary-like systems, such as proposed for the Sarmatian section, benthic mass-mortalities are frequently caused by the breakdown of water circulation, eutrophication and hypoxia. (Yamamuro et al. 2000; Zwaan and Babarro 2001; Zwaan et al 2002; Kauppila et al. 2003). This hypoxia-scenario is supported by the concretions within and around the solenid shells, pointing to decaying processes within-habitat in an anoxic environment.

Such events are frequently linked with the establishment of a thermocline during summer, affecting the bottom water of the estuarine ecosystem. Experiments in oyster reefs in the Neuse River estuary in North Carolina, for example, documented an increase in mortality from zero at the surface to ca. 28% at 3 m to ca. 92% in 6-m water depth (Lenihan and Peterson 1998). This thermocline model, however, cannot be applied for the intertidal solenid-batillariid assemblage, which would have been unaffected by such sublittoral hypoxia. An alternative scenario, affecting also tidal communities by hypoxia, would be a bloom of macroalgae (green tides) as described from the German Wadden Sea and several other settings (Kolbe et al. 1995; Morand and Merceron 2005).

Algal overproduction in estuarine lagoons is initiated by high nutrient influx from land and restricted water exchange with the open sea (Morand and Merceron 2005). Such blooms can virtually eliminate infaunal bivalves from the ecosystem as shown by the experiments with *Macoma* in Bodega Harbor in California (Everett 1991). Interestingly, the hypoxia produced by subsequent algal decay is not the primary cause for the benthic mass-mortalities. Instead, bivalves such as *Macoma* or *Cerastoderma* are killed by severe bacterial infection as a consequence of bacterial outbreaks that are part of every benthic anoxic event (Zwaan and Barbarro 2001).

Granulolabium bicinctum taphofacies—a hint at pagurization?

The medium to small-sized, turreted gastropod is commonly documented in an aperture-up position with the shell axis forming an angle of about 60°–80° to the surface (Fig. 5f). This strange position of *Granulolabium bicinctum* is bound to the topmost part of fine sandy layers which are topped by pelitic layers. The shells occur very close to the

pelites or sometimes even penetrate their lowermost part. This position also rarely occurs within pelites. Typically, a small subspherical limonitic concretion forms at the aperture. These concretions are interpreted to derive originally from iron-sulfides which developed from decaying organic material in a poorly oxygenized environment (Allison 1988; Allen 2002). Following this interpretation, the shells were inhabited during the sedimentation either by the gastropods or by some other organism. Thus, a simple physical trigger such as small-scale current-vortices for the orientation, as suggested by Klinger (1931) and Krejci-Graf (1932), can be ruled out. In contrast, Schwarz (1931) and Papp (1948) preferred biological mechanisms as an explanation and discussed rapid covering by sediment of living gastropods and their subsequent attempt to re-bury. This interpretation might apply for some findings within the sand such as illustrated in Fig. 5f. For most cases, however, a very quick covering by sediment as supposed by Papp (1948) is problematic. Many specimens are found at the sand/pelite interface or even within pelites. The covering by rather slowly depositing pelites seems to contradict a rapid burial. In addition, a distinct erosional boundary is usually developed between the sand and the overlying pelites. Thus the layers represent two different episodes of deposition and cannot be treated as a single event with graded bedding. In any case, modern relatives of *Granulolabium* are epifaunal browsers in the intertidal zone, where they form large populations in the low tide zone under permanent water flow (Lozouet et al. 2001). They do not penetrate into the sediment and thus the fossil shells cannot be interpreted to reflect the life position of the animals. Based on these data, we exclude (1). that the position of the shells reflects a life-position of *Granulolabium* and (2). that the gastropods were rapidly covered and thereafter tried to escape. This is supported by the fact that strictly epifaunal neritid gastropods (Fig. 5, 7) are rarely found in a similar position with a concretion at the aperture.

A second interpretation is that sipunculids could have settled the *Granulolabium* shells. Among modern sipunculans, *Aspidosiphon* Diesing 1851 and *Phascolion* Théel 1875 frequently occupy empty gastropod shells (Cutler 1994). Especially *Phascolion* is of major interest with respect to the Sarmatian occurrences. Some species form cone-shaped extensions of agglutinated sand grains at the aperture; these could have been the nuclei for the typical limonitic sandy concretions at the apertures of *Granulolabium bicinctum*. However, the epifaunal mode of life of all *Aspidosiphon* and *Phascolion* species contradicts the apparently infaunal position of the enigmatic occurrence.

Therefore, it is more likely that sediment-dwelling organisms such as hermit crabs inhabited the shells. Among the hermit crabs, only representatives of the families Diogenidae Ortmann 1892 and Paguridae Latreille 1802 are

potential candidates based on habitat and body-size. Both families contain psammophilic species which favour intertidal environments where they bury themselves in a circadian rhythm and are also confronted with hypoxic events (Côté et al. 1998; Asakura 1991; McGrath et al. 2000; Turra and Denadai 2003). A very close modern counterpart was described by Wonham et al. (2005) from mudflats in the NW Pacific. There, the Asian hornsnail *Batillaria attramentaria* (Sowerby 1855) is settled by *Pagurus hirsutiusculus* (Dana 1851) and *P. granosimanus* (Stimpson 1859). At first glance, this interpretation seems to be unlikely as no crustaceans are documented from the Sarmatian of the Central Paratethys (Müller 1998) aside from a biostratigraphically very limited horizon with mysid statoliths (Fuchs 1979; Voicu 1981). Nevertheless, the position of the gastropod shells and their obligatory concretions render hermit crabs as very likely producers of that taphonomic structures. The small size and the poor calcification of the carapaces may explain the complete taphonomic loss. The crabs' selective use of a single host species is easily understandable considering the documented mollusc fauna. Aside from the rarely utilized neritid shells, only *Granulolabium* is present in conspicuous amounts and fits in size to diogenid or pagurid hermit crabs. In contrast, the hydrobiids and *Mohrensternia* are too small to serve as housing, whereas *Turritella* and the other larger-sized gastropod shells are very rare.

Depositional history

In the eastern surroundings of Hollabrunn, gravels are frequently intercalated in a 100 to 200-m-thick fine-grained succession of the Early Sarmatian. They derived most probably from the Middle to Late Badenian, valley-incising palaeo-Zaya river system, and were reworked during the low stand systems tract of the lowermost Sarmatian (Roetzel 2003, 2007a, b). At Siebenhirten near Mistelbach (Harzhauser and Piller 2004b), similar Sarmatian gravel indicates the transition of a deltaic complex into the Vienna Basin. During the subsequent Early Sarmatian transgression the incised valley was reactivated as a marine lough of the Central Paratethys Sea, visible at the Hollabrunn/Aspersdorf section by the reworking of gravel in Unit 1. The exotic, biostratigraphically condensed assemblage (Kidwell and Bosence 1991) comprises terrestrial gastropods and Badenian oysters along with Karpatian and Badenian microfossils (foraminifers, ostracods); this implies terrestrial input and intensive reworking of older deposits. Soon thereafter, the exceptional palaeogeographic situation of a very narrow long embayment in a low-relief topography (Fig. 2) favoured the establishment of tideland environments with flat coasts (Fig. 8). Mud clasts along with frequent

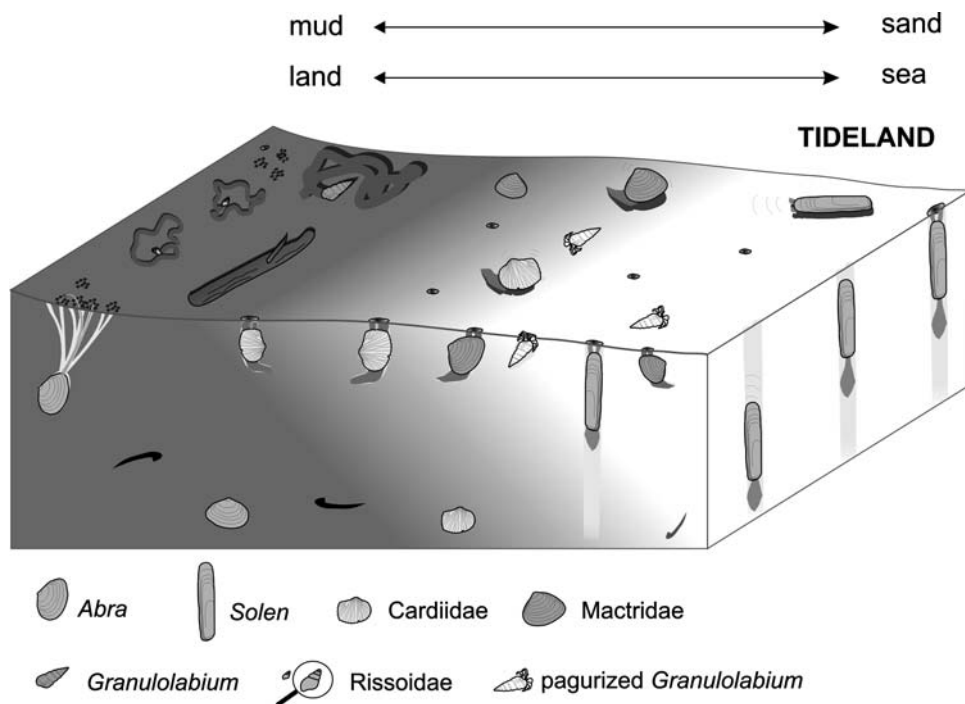


Fig. 8 Sketch showing habitat distributions and mode of life of characteristic molluscs represented in the studied section. Muddy areas covered by diatom-mats were preferably occupied by *Abra*, *Mohrensternia* and *Granulolabium*. Mixed to sandy flats were preferred by cardiids and mactrids, whereas sandy areas in the lowermost intertidal to uppermost subtidal zone were occupied by dense solenid colonies.

Granulolabium shells therefore imply out-of-habitat reworking of intertidal mud flat sediments, probably during higher energetic phases. Spectacular convolute bedding and water escape structures characterize the overlying units (Unit 2, 3) in the Hollabrunn/Aspersdorf section. This is a predominantly fine-sand succession with intercalated pelitic horizons, bearing a within-habitat, time-averaged mollusc assemblage (Kidwell and Bosence 1991) from an intertidal or shallow subtidal habitat zone. The next unit (Unit 4), starting with gravel-bearing medium to fine sands, levels the top of the previous unit and comprises an intensive pelite/sand interchange. The intensive bioturbation by solenid bivalves, commonly preserved in life position, points to a lower intertidal sedimentary environment within a less energetic water regime. The occurrence of the bivalves is interpreted as a census assemblage with only minor within-habitat time-averaging (Kidwell and Bosence 1991). In contrast, the following 70 cm fine to medium sandy unit (Unit 5) displays ripple cross bedding and planar lamination. This marks the shift towards higher water energy in a shallow subtidal, possibly wave-influenced environment. No in situ occurrences of molluscs occur, whereas mollusc debris predominates. The final retreat of the sea is indicated by the re-installation of intertidal mud plain conditions in the muddy top of the succession. Here, the occurrence of

Solenids are shown as swimmers and suspension feeders capable for deep burrowing when disturbed. Mactrids and cardiids are shallowly burrowing filter feeders that can move on the sediment surface by jumping. *Abra* is a very fast, deep burrower which is a predominant deposit feeder and thus an intensive pellet producer. *Granulolabium* lives on the sediment surface, where it crawls and feeds on algal mats

the herbivorous gastropod *Granulolabium* points to the formation of algal mats (Unit 6). Evidence of direct freshwater influx, as might be deduced from riverine or lacustrine molluscs, is missing. This might reflect the palaeogeographic position of the outcrop in the seaside half of the incised valley, about 30 km off the estuary head, near Krems (Papp 1962). There, the correlative Lower Sarmatian deposits yield fluvial molluscs (Milles and Papp 1957) and thus reflect stronger riverine influx. As shown by Branch and Branch (1981), the influence of the riverine influx on salinity decreases considerably from the head to the mouth of the estuary, being usually higher than 15‰ in its distal half.

We suggest that the presented environmental evolution is related to sea-level fluctuations of the Central Paratethys Sea rather than to autocyclic processes. The development starts with the flooding during the initial Sarmatian transgression, reflected by the basal gravely deposits. A subsequent, rapid sea-level rise culminated in the maximum flooding expressed by the wave- and current-dominated Unit 5. Hence, the backshore environments of Unit 1 were replaced by a foreshore which was developed as a sandy to muddy tidal flat during the deposition of Units 2–4. The diverse sedimentary structures and taphonomic features of Unit 5 indicate deposition within the shoreface. The forma-

tion of the conspicuous solenid bivalve colonies is thus related to the Lower Sarmatian transgressive systems tract, pushing back the fluvial drainage of the foreland basin. The corresponding early Sarmatian highstand is reflected by the gradual shallowing of the inlet and the renewed development of vast tidal flats.

Conclusions

The palaeogeographic position of the investigated section was at the western margin of the Central Paratethys Sea, which extended here about 50 km from the Vienna Basin to the west into the otherwise already dry North Alpine Foreland Basin. It represents one of the northwestern-most Sarmatian sections of the Central Paratethys and was part of an ancient incised valley. This unusually long and narrow embayment was prone to rapid environmental changes due to shifts in water circulation and regional sea-level fluctuations.

The studied section documents a very rare case of within-habitat occurrences of Early Sarmatian mollusc assemblages soon after the major extinction event at the Badenian/Sarmatian boundary. The composition shows that the still impoverished benthic faunas were dominated by few taxa such as solenid and macrid bivalves and batillariid gastropods. Moreover, the section yields the only known census-assemblages from that time interval in the Central Paratethys Sea and points to frequent benthic mass-mortalities in selected intertidal areas.

In situ occurrences with traces of former iron-sulfide concretions strongly suggest hypoxic events as the cause for the mass-mortalities on the tidal-flats. In modern estuaries and intertidal zones, such tidal-flat hypoxias typically occur during green tides (Morand and Merceron 2005). Such algal blooms are responses to eutrophication due to elevated loads of nutrients and organic carbon. The geomorphology of the incised valley, producing a very narrow but elongated marine inlet, suggests that the water body was influenced by shifts in freshwater discharge, which was responsible for that loading. Similarly, the water current system of such a shallow inlet was unstable and strongly depended on the relative sea level. This induced periodic isolation events supporting eutrophication. Consequently, the associated faunas are expected to reflect changes of these parameters quickly, especially considering the rapidly oscillating relative sea level of the Early Sarmatian (Harzhauser and Piller 2004a).

Whilst the in situ solenid occurrences can be unequivocally attributed to bivalves, the strange position of the *Granulolabium* shells excludes the gastropods as producers. Instead, such taphonomic feature is apparently caused by diogenid or pagurid hermit crabs, which are known to

choose batillariid gastropod shells in modern tidal flats (Wonham et al. 2005). This interpretation would add another group to the few survivors of the Badenian/Sarmatian extinction event. With respect to the nearly completely missing Sarmatian decapod crustaceans, the proof of Paguridae has an important impact on further reconstructions of Sarmatian marine ecosystems.

Acknowledgments This investigation was part of the excavation campaign by the Department of Paleontology, University of Vienna, organized by Fritz F. Steininger and Peter Pervesler. The paper is a contribution to FWF project P19013 and to the NECLIME project.

References

- Allen RE (2002) Role of diffusion–precipitation reactions in authigenic pyritization. *Chem Geol* 182:461–472
- Allison PA (1988) The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Paleobiology* 14:139–154
- Asakura A (1991) Population ecology of the sand-dwelling hermit crab *Diogenes mitidiamus*. IV. Larval settlement. *Mar Ecol Prog Ser* 78:139–146
- Baráth I, Kovác M (2000) Miocene sequence stratigraphic key surfaces and depositional system tracts in the Western Carpathian basins (Central Paratethys, Slovakia). *Slovak Geol Mag* 6:92–94
- Basterot B (1825) Description géologique du bassin tertiaire du S.O. de la France. *Mémoire de la Société de Histoire Naturelle, Paris* 11, 100 pp
- Bazas MA, Carle KJ (1979) Predators of foraminifera in the Indian River, Florida. *J Foraminiferal Res* 9:336–340
- Bittner A (1883) Ueber den Charakter der sarmatischen Fauna des Wiener Beckens. *Jahrbuch der k.k. Geologischen Reichsanstalt* 33:131–150
- Boettger O (1884) Fossile Binnenschnecken aus den untermiocänen *Corbicula*-Thonen von Nierrhein bei Frankfurt (Main). *Berichte der senckenbergischen naturforschenden Gesellschaft* 1884:256–280
- Bourguignat JR (1881) Histoire malacologique de la colline de Sansan precedee d'une notice geologique et suivie d'un aperçu climatologique et topographique de Sansan, a l'epoque des depots de cette colline. G. Masson, Paris, 175 pp
- Branch M, Branch G (1981) The living shores of Southern Africa. Cape Town, Struik, 272 pp
- Brocchi GV (1814) Conchiologia fossile subapennina, con osservazioni sugli Appenini e sul suolo adjacente. Dalla Stamperia Reale, Milano, 712 pp
- Cadee GC (2000) Herring gulls feeding on a recent invader in the Wadden Sea, *Enis directus* in kursiv. In: Harper EM, Taylor JD, Crame JA (eds) The evolutionary biology of the Bivalvia. *Geol Soc Lond, Spec Publ*, vol 177, pp 459–464
- Clessin S (1877) Die tertiären Binnenconchylien von Undorf. *Correspondenz-Blatt des zoologischen und mineralogischen Vereins in Regensburg* 1877:71–95
- Conrad TA (1843) Descriptions of nineteen species of Tertiary fossils of Virginia and North Carolina. *Proc Acad Nat Sci Philadelphia* 1:323–329
- Côté IM, Benedicte R, Cooke PK (1998) Less choosy or different preference? Impact of hypoxia on hermit crab shell assessment and selection. *Anim Behav* 56:867–873
- Cutler EB (1994) The Sipuncula. Their systematics, biology, and evolution. Comstock Publishing associates, Cornell University Press, Ithaca, 453 pp

- Dalrymple RW, Boyd R, Zaitlin BA (1994) History of research, definitions and internal organization of incised-valley systems: introduction to the volume. In: Dalrymple RW, Boyd R, Zaitlin BA (eds) Incised-valley systems: origin and sedimentary sequences. SEPM Special Publications, vol 51, pp 3–10
- Dana JD (1851) 1. On the classification of the Cancroidea. *Silliman's Am J Sci Arts Ser 2*, 12:121–131
- Diesing KM (1851) *Systema helminthum*. Vindobonae 1/2:1–588
- Dixon G (1789) A voyage round the World; but more particularly to the north-west coast of America performed by order of His Most Christian Majesty, in the years 1785, 1786, 1787 and 1788, in the King George and Queen Charlotte, by captains Portlock and Dixon, Londres, Goulding, 1789, 4 volumes (not seen)
- Eichwald E (1830) Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht. Wilna, Voss, pp 256
- Eichwald E (1853) *Lethaea Rossica ou Paléontologie de la Russie 3*, dernière période. Schweitzerbart, Stuttgart, 533 pp
- Everett RA (1991) Intertidal distribution of infauna in a central California lagoon: the role of seasonal blooms of macroalgae. *J Exp Mar Biol Ecol* 150:223–247
- Fischer P (1881) Manuel de conchyliologie et de paléontologie conchyliologique on histoire naturelle des mollusques vivants et fossiles. II Distribution géographique des mollusques. Savy, Paris, pp 113–192
- Fechter R, Falkner G (1989) Weichtiere. In: Steinbach G (ed) *Die farbigen Naturführer*, München, Mosaik, 287 pp
- Friedberg W (1934) *Mollusca miocaenica Poloniae*. Pars II. Lamellibranchiaten, 1. Lieferung, Krakow, 158 pp
- Fuchs R (1979) Das Vorkommen von Statolithen fossiler Mysiden (Crustacea) im obersten Sarmatium (O-Miozän) der Zentralen Paratethys. *Beiträge zur Paläontologie Österreichs* 6:61–69
- Fuchs W, Grill R, Matura A, Vasicek W (1984) Geologische Karte der Republik Österreich 1:50.000 38 Krems. Geologische Bundesanstalt
- Füchtbauer H (1959) Zur Nomenklatur der Sedimentgesteine. *Erdöl und Kohle* 12:605–613
- Glaister RP, Nelson HW (1974) Grain-size distributions, an aid in facies identification. *Bull Can Petrol Geol* 22:203–240
- Gottschick F (1911) Aus dem Tertiärbecken von Steinheim a. A. Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg 66:496–534
- Grill R (1968) Erläuterungen zur Geologischen Karte des nordöstlichen Weinviertels und zu Blatt Gänserndorf, Wien, Geologische Bundesanstalt, 155 pp
- Haq BU, Hardenbol J, Vail PR (1988) Mesozoic and Cenozoic chronostratigraphy and cycles of sea level changes. *SEPM Spec Publ* 42:71–108
- Harbeck K (1996) Die Evolution der Archaeopulmonata. *Zoologische Verhandlungen* 305:1–133
- Hardenbol J, Thierry J, Farley MB, Jaquin TH, Vail PR (1998) Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. *SEPM Spec Publ* 60:1–13
- Harzhauser M, Kowalke T (2002) Sarmatian (Late Middle Miocene) gastropod assemblages of the Central Paratethys. *Facies* 46:57–82
- Harzhauser M, Piller WE (2004a) The Early Sarmatian—hidden sea-saw changes. *Courier Forschungsinstitut Senckenberg* 246:89–111
- Harzhauser M, Piller WE (2004b) Integrated stratigraphy of the Sarmatian (Upper Middle Miocene) in the western Central Paratethys. *Stratigraphy* 1:65–86
- Harzhauser M, Piller WE (2007) Benchmark data of a changing sea. Palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeogr Palaeoclimatol Palaeoecol* 253:8–31
- Harzhauser M, Daxner-Höck G, Boon-Kristkoiz E, Coric S, Mandic O, Miklas-Tempfer P, Roetzel R, Rögl F, Schultz O, Spezzaferri S, Ziegler R, Zorn I (2003) Paleoeecology and biostratigraphy of the Gaidorf formation (lower Middle Miocene, Lower Badenian, Austria). *Annalen des Naturhistorischen Museums in Wien* 104A:323–334
- Hertweck G (1990) Die Zonierung der Lebensspuren im Watt der Jade, südliche Nordsee. *Beiträge zur Geologie und Paläontologie N-Deutschlands* 10:159–188
- Hilber V (1897) Die sarmatischen Schichten vom Waldhof bei Wetzelndorf, SW Graz. *Mitteilungen des Naturwissenschaftlichen Vereins der Steiermark* 33:182–204
- Jiriček R, Seifert P (1990) Palaeogeography of the Neogene in the Vienna Basin and the adjacent part of the foredeep. In: Minaříková D, Lobitzer H (eds) Thirty years of geological cooperation between Austria and Czechoslovakia, Praha, pp 89–105
- Kaupilla P, Meeuwig JJ, Pitkänen H (2003) Predicting oxygen in small estuaries of the Baltic Sea: a comparative approach. *Estuar Coast Shelf Sci* 57:1–12
- Kidwell SM, Bosence DWJ (1991) Taphonomy and time-averaging of marine shelly faunas. In: Allison PA, Briggs DEG (eds) Taphonomy: releasing the data locked in the fossil record. Plenum Press, New York, Topics in Geobiology 9:115–209
- Klinger FE (1931) Sedimentationsstörungen durch “Wasserkegel” in sarmatischen Schichten. *Senckenbergiana* 13:52–59
- Kolbe K, Kaminski E, Michaelis H, Obert B, Rahmel J (1995) Macroalgal mass development in the Wadden Sea: first experiences with a monitoring system. *Helgoländer Meeresuntersuchungen* 49:519–528
- Kowalke T, Harzhauser M (2004) Early ontogeny and palaeoecology of the Mid-Miocene rissoid gastropods of the Central Paratethys. *Acta Palaeontol Pol* 49:111–134
- Krejci-Graf K (1932) Senkrechte Regelung von Schneckengehäusen. *Senckenbergiana* 14:295–299
- Kojumdžieva E (1960) Le Tortonien du type viennois. In: Kojumdžieva E, Strachimirov B (eds) *Le fossiles de Bulgarie, VII, Tortonien*. Academie sciences des Bulgarie, Sofia, 246 pp
- Lamarck J-BPA de (1818) Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s’y rapportent; précédée d’une introduction offrant la détermination des caractères essentiels de l’animal, sa distinction du végétal et des autres corps naturels, enfin, l’exposition des principes fondamentaux de la zoologie. Paris, Deterville, Verdier 5:1–612
- Laskarev VD (1903) Die Fauna der Buglowka-Schichten in Volhynien. *Mémoires du Comité Géologique, Nov. série* 5, 28:1–148
- Laskarev VD (1914) Obtaja geologičeskaja karta Evropejskoj Rossii. List 17. *Mémoires du Comité Géologique, Nov. série* 77:1–730
- Latreille PA (1802) Histoire naturelle, generale et particuliere, des Crustacés et des Insectes. F. Durart, Paris 3:1–468
- Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol Appl* 8:128–140
- Ložek V (1964) Quartärmollusken der Tschechoslowakei. *Rozpravy Ústředního Ústavu Geologického* 31:1–374
- Lozouet P, Lesport J-F, Renard P (2001) Révision des Gastropoda (Mollusca) du Stratotype de l’Aquitainen (Miocène inf.): site de Saucats “Lariey”, Gironde, France. *Cossmanniana* 3:1–189
- Lueger JP (1981) Die Landschnecken im Pannon und Pont des Wiener Beckens, I. Systematik. II. Fundorte, Stratigraphie, Faunenprovinzen. *Denkschriften der Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* 120:1–124
- Mandic O, Harzhauser M, Spezzaferri S, Zuschin M (2002) The paleoenvironment of an early Middle Miocene Paratethys sequence in NE Austria with special emphasis on paleoecology of molluscs and foraminifera. *Geobios, Memoire special* 24:193–206

- McGrath D, Costello MJ, Emblow C (2000) The hermit crab *Diogenes pugilator* (Roux, 1829) in Irish waters. *Biol Environ Proc Ro Irish Acad* 100B:115–118
- Milišić N (1991) Školjke i puževi Jadrana. Split, Logos, 302 pp
- Miller K (1900) Die Schneckenfauna des Steinheimer Obermiozäns. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 56:385–406
- Milles R, Papp A (1957) Über das Vorkommen sarmatischer Schichten im Außer-alpinen Wiener Becken. *Verhandlungen der Geologischen Bundesanstalt* 1957:130–136
- Morand P, Merceron M (2005) Macroalgal population and sustainability. *J Coast Res* 21:1009–1020
- Müller G (1961) Das Sand-Silt-Ton-Verhältnis in rezenten marinen Sedimenten. *Neues Jahrbuch Mineralogie, Monatshefte*, 1961:148–163
- Müller OF (1774) Vermium terrestrium et fluviatilium, seu animalium infusorium, helminthicorum et testaceorum, non marinorum, succincta historia. *Havniae, Heineck & Faber* 2:1–214
- Müller P (1998) Crustacea Decapoda. *Catalogus Fossilium Austriae*, Wien, Österreichische Akademie der Wissenschaften VIII/2b:1–48
- Neveskaja LA, Goncharova IA, Paramonova NP, Popov SB, Babak EB, Bagdasarjan KG, Voronina AA (1993) Opređelitelj miocenovjih dvustvorchatjih molljuskov Jugo-Zapadnoi Evrazii. Moskva, Nauka, 412 pp
- Ortmann A (1892) Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und z.Z. im Strassburger Museum aufbewahrten Formen. V. Theil. Die Abteilungen Hippidea, Dromiidea und Oxystomata. *Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere* 6:532–588
- Papp A (1948) Die senkrechte Einregelung von Gastropodengehäusen in Tertiärschichten des Wiener Beckens. *Palaeobiologica* 8:144–153
- Papp A (1950) Das Sarmat von Hollabrunn. *Verhandlungen der Geologischen Bundesanstalt* 1948:110–112
- Papp A (1951) Über die Altersstellung der Tertiärschichten von Lischta bei Prävali und Lobnig. *Carinthia* 61:62–64
- Papp A (1954) Die Molluskenfauna im Sarmat des Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien* 45:1–112
- Papp A (1956) Fazies und Gliederung des Sarmats im Wiener Becken. *Mitteilungen der Geologischen Gesellschaft in Wien* 47:1–97
- Papp A (1962) Über das Vorkommen sarmatischer Schichten bei Langenlois am Kamp (N-Ö). *Verhandlungen der Geologischen Bundesanstalt* 1962:361–363
- Papp A, Steininger F (1974) Faziostratotypus: Hollabrunn, N. Ö. (früher Ober-Hollabrunn), Wiener Becken, Österreich. In: Papp A, Marinescu F, Seneš J (eds) *M₅ Sarmatien. Chronostratigraphie und Neostratotypen* 4:172–176
- Pennant T (1777) *British Zoology*. Vol. IV. Crustacea. Mollusca. Testacea. London, White, pp 1–154
- Perillo GME (1995) Geomorphology and sedimentology of estuaries. An introduction. In: Perillo GME (ed) *Geomorphology and sedimentology of estuaries*. *Dev Sedimentol* 53:1–16
- Piller WE, Harzhauser M (2005) The myth of the brackish Sarmatian Sea. *Terra Nova* 17:450–455
- Piller WE, Harzhauser M, Mandic O (2007) Miocene Central Paratethys stratigraphy—current status and future directions. *Stratigraphy* 4:151–168
- Poppe GT, Goto Y (1993) *European Seashells*. vol II (Scaphopoda, Bivalvia, Cephalopoda). Wiesbaden, Christa Hemmen Verlag, pp 221
- Reuss A (1849) Die tertiären Süßwassergebilde des nördlichen Böhmens und ihre fossilen Thierreste II. Beschreibung der fossilen Ostracoden und Mollusken der tertiären Süßwasserschichten des nördlichen Böhmens. *Palaeontographica* 2:16–42
- Roetzel R (1998) Geologische Karte der Republik Österreich 1:50.000 22 Hollabrunn. Geologische Bundesanstalt
- Roetzel R (2003) Bericht 1998, 2000 und 2001 über geologische Aufnahmen im Tertiär und Quartär auf Blatt 23 Hadres. *Jahrbuch der Geologischen Bundesanstalt* 143:397–404
- Roetzel R (2007a) Bericht 2002, 2003, 2004, 2005 und 2006 über geologische Aufnahmen im Tertiär und Quartär auf Blatt 23 Hadres. *Jahrbuch der Geologischen Bundesanstalt* 147:615–623
- Roetzel R (2007b) Geologische Karte der Republik Österreich 1:50.000 23 Hadres. Geologische Bundesanstalt
- Schütt H (1967) Die Landschnecken der untersarmatischen Rissoenschichten von Hollabrunn, N.Ö. *Archiv für Molluskenkunde* 96:199–222
- Schwarz A (1931) Sedimentationsstörungen durch “Wasserkegel” in sarmatischen Sanden. Kritische Bemerkungen zum Klingerschen Erklärungsversuch. *Senckenbergiana* 13:243–248
- Schultz O (2001) Bivalvia neogenica (Nuculacea-Unionacea). In: Piller WE (ed) *Catalogus Fossilium Austriae* 1/1:1–379
- Shonman D, Nybakken JW (1978) Food preferences, food availability and food resource partitioning in two sympatric species of cephalopod gastropods. *The Veliger* 21:120–126
- Sindowski K-H (1957) Die synoptische Methode des Kornkurven-Vergleiches zur Ausdeutung fossiler Sedimentationsräume. *Geologisches Jahrbuch* 73:235–275
- Sowerby GB (1855) *Thesaurus Conchyliorum, or monographs of genera of shells*. London 1/2:1–899
- Stanley SM (1970) Relation of shell form to life of the Bivalvia (Mollusca). *Memoir GSA* 125:1–296
- Stimpson W (1859) Notes on North American Crustacea, No. 1. *Ann Lyceum Nat Hist New York* 7:49–93
- Strauss P, Harzhauser M, Hinsch R, Wägrich M (2006) Sequence stratigraphy in a classic pull-apart basin (Neogene, Vienna Basin). A 3D seismic based integrated approach. *Geologica Carpathica* 57:185–197
- Suess E (1866) Untersuchungen über den Charakter der österreichischen Tertiärlagerungen. II. Über die Bedeutung der sogenannten “brackischen Stufe” oder der “Cerithienschichten”. *Sitzungsberichte der k.k. Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* 54:1–40
- Tegelberg HC, Magoon CD (1969) Growth, survival, and some effects of a dense razor clam set in Washington. *Proc Nat Shellfish Assoc* 59:126–135
- Théel H (1875) Études sur les géphyriens inermes des mers de la Scandinavie, du Spitzberg et du Groënland. *Kungliga Svenska Vetenskapsakademien, Stockholm*, 30 pp
- Turra A, Denadai MR (2003) Daily activity of four tropical intertidal hermit crabs from southeastern Brazil. *Braz J Biol* 63:537–544
- Vetters H (1914) Mitteilungen aus dem tertiären Hügellande unter dem Manhartsberge. *Verhandlungen der Geologischen Reichsanstalt* 1914:65–74
- Visher GS (1969) Grain size distributions and depositional processes. *J Sediment Petrol* 39:1074–1106
- Visher GS, Howard JD (1974) Dynamic relationship between hydraulics and sedimentation in the Altamaha Estuary. *J Sediment Petrol* 44:502–521
- Voicu G (1981) Upper Miocene and recent mysid statoliths in Central and Eastern Paratethys. *Micropaleontology* 27:227–247
- Wenz W (1919) Zur Nomenklatur tertiärer Land- und Süßwassergastropoden. *Nachrichtenblatt der deutschen malakologischen Gesellschaft* 51:76–79
- Willmann R (1989) *Muscheln und Schnecken der Nord- und Ostsee*. Melsungen, Neumann-Neudamm, 310 pp

- Wonham MJ, O'Connor M, Harley CDG (2005) Positive effects of a dominant invader on introduced and native mudflat species. *Mar Ecol Prog Ser* 289:109–116
- Yamamuro M, Hirutsuka J, Ishitobi Y (2000) Seasonal change in a filter-feeding bivalve *Musculista senhousia* population of a eutrophic estuarine lagoon. *J Mar Sys* 26:117–126
- Zwaan A de, Babarro JMF (2001) Studies on the causes of mortality of the estuarine bivalve *Macoma balthica* under conditions of (near) anoxia. *Mar Biol* 138:1021–1028
- Zwaan A de, Babarro JMF, Monari M, Cattani O (2002) Anoxic survival potential of bivalves: (arte)facts. *Comp Biochem Physiol A* 131:615–624