Bivalves from the Middle Miocene reefs of Poland and Ukraine: A new approach to Badenian/Sarmatian boundary in the Paratethys

BARBARA STUDENCKA¹ AND MAREK JASIONOWSKI 2

¹ Polish Academy of Sciences Museum of the Earth in Warsaw, Al. Na Skarpie 20/26, PL-00-488 Warsaw, Poland. E-mail: bstudencka@go2.pl

ABSTRACT:

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The Late Badenian coralline algae-vermetid reefs and the Early Sarmatian serpulid-microbialite reefs distributed widely in the northeastern and eastern borders of the Carpathian Foredeep Basin contain an excellent bivalve record and show how the bivalve faunas reflected the temporary closure of seaways between the Paratethys and the Mediterranean around 13.3 Ma. Within the Late Badenian reefs, 116 bivalve species and three bivalve associations are recognized. After a dramatic change of environmental factors, the Early Sarmatian reefs hosted 12 bivalve species, grouped in four associations. These are thought to have been controlled largely by salinity and to represent decreased and/or fluctuating salinity regimes.

An integrated approach, using benthic fauna, sedimentological and isotope data, enabled interpretation of the origin of the serpulid-microbialite reefs.

The changes in the palaeogeography of the Paratethys and sea-level oscillations around the Badenian/Sarmatian boundary played an important role in the distribution, extinction and radiation of the bivalves. The definitive closure of the extensive seaway connecting the Paratethys with the Mediterranean caused not only severe extinction of the bivalves inhabiting the sandy facies during the Late Badenian but also the sudden evolution and dispersal of a few opportunistic species that were ancestral forms to Sarmatian taxa. The composition of the bivalve assemblages and the ecological requirements of particular species prove the mixo-mesohaline character of the Sarmatian Sea (30–18‰) and indicate an eastward decrease in salinity.

Key words: Bivalves; Coralline algae-vermetid and serpulid-microbialite reefs; Badenian/Sarmatian extinction event; Salinity; Paratethys.

INTRODUCTION

The history of the Paratethys, a vast inland sea that existed from the earliest Oligocene until the Pliocene, is marked by intermittent openings and closings of marine seaways towards the Mediterranean, the Indo-Pacific region of Tethys, and the Atlantic (e.g. Nevesskaja *et al.* 1986, 1987, 2005; Rögl 1998, 1999; Steinninger and Wessely 2000; Meulenkamp and Sissingh 2003 and

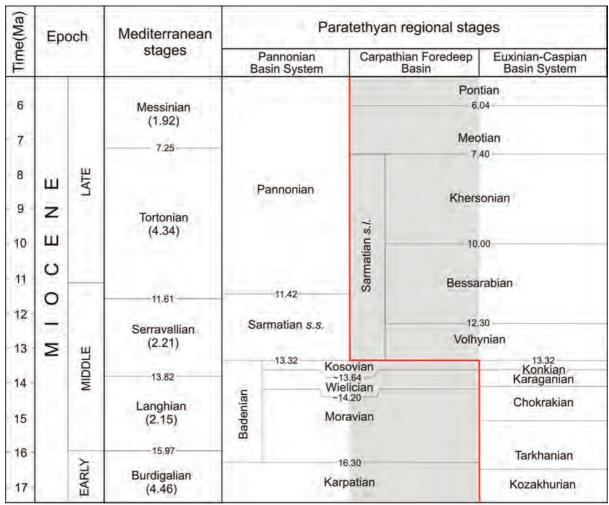
Popov *et al.* 2004). Closures of wide connections between the Paratethys and the world ocean considerably changed both the palaeogeography of the Paratethyan basins and their environmental factors such as salinity, temperature, stratification of the water column, conditions at the sea bottom, and directions of surface and deep-water currents. Consequently, strong endemism within the shallow-water fauna is often observed throughout the Paratethys. Hence, the stratigraphy of the Paratethys is determined

² Polish Geological Institute-National Research Institute, ul. Rakowiecka 4, PL-00-975 Warsaw, Poland. E-mail: marek.jasionowski@pgi.gov.pl

largely by its palaeogeographic history, and different regional stage systems are used for the Central and the Eastern parts of the Paratethys (Text-fig. 1).

In the Central Paratethys, as demonstrated by Kováč *et al.* (2007), the last period of fully marine conditions took place in the Late Badenian, a time span roughly correlated with the early Serravallian. The base of the Late Badenian Substage corresponds to the first appearance of the planktonic foraminifer *Velapertina indigena* (Łuczkowska), but its precise age is still disputable. It can be estimated as about 13.64 Ma (see Kováč *et al.* 2007) while the recently revised age of the Badenian/Sarmatian boundary was astronomically dated at 13.32 Ma by Lirer *et al.* (2009).

The Late Badenian transgression is documented throughout the Pannonian Basin System (Kováč et al. 2007), in both the northern and eastern parts of the Carpathian Foredeep Basin (Musiał 1987; Krzywiec 2001; Oszczypko et al. 2005; Oszczypko 2006), and along the southwestern margin of the East European Platform over a vast area of the Volhynian and Podolian regions of western Ukraine (Andreyeva-Grigorovich et al. 1997). In addition, a short-lived connection between the Central and Eastern Paratethys was re-established at that time (Didkovsky and Nosovsky 1975; Studencka et al. 1998; Krasheninnikov et al. 2003; Popov et al. 2004). The geological record indicates the presence of the Predobrogean



Text-fig. 1. Correlation chart of the Miocene regional stages of the Central and Eastern Paratethys and Mediterranean province. The chronology of the Mediterranean stages after the ICS chart (2009). Position of the Karpatian/Badenian boundary according to Kovač *et al.* (2007), age of the Badenian/Sarmatian and Sarmatian/Pannonian boundaries after Lirer *et al.* (2009). Position of the Volhynian/Bessarabian, Bessarabian/Khersonian and Khersonian/Meotian boundaries after Popov *et al.* 2006 and the Meotian/Pontian boundary after Krijgsman *et al.* 2010. There is some disagreement about stratigraphic correlation between the Central and Eastern Paratethyan Sarmatian stages. In this paper Sarmatian is used in the sense recommended by the working group on Paratethys of the Committee on Mediterranean Neogene Stratigraphy (Seneš 1974). Following this recommendation, the Sarmatian *sensu stricto* [Sarmatian *sensu* Seuess] is the regional stage of the Central Paratethys whilst the Sarmatian *sensu lato* [Sarmatian *sensu* lato [Sarmatian *sensu*] lato [Sarmatian *se*

Strait (between the Podolian Massif and the Moesian Platform) towards the Eastern Paratethys (Roshka and Khubka 1981; Gontsharova and Iljina 1997). The location of a passage linking the Central Paratethys with the Mediterranean is still disputable (see Kókay 1985; Gontsharova and Shcherba 1997; Rögl 1998, 1999; Studencka *et al.* 1998; Studencka 2001 and Kováč *et al.* 2007).

At the Badenian/Sarmatian boundary, the connection to the Mediterranean became strongly restricted, which caused limited water exchange between the Paratethys and the world ocean.

This paper is intended to show how the species composition and the taxonomic structure of the bivalve fauna populating the Late Badenian Sea reflected the temporary closure of seaways between the Paratethys and the Mediterranean area around 13.3 Ma.

Analyses of the bivalve fossil assemblages demonstrate that the nature of the substrate had a profound effect on the taxonomic structure. The bivalve assemblages from the carbonates not only differ in the number of species from those coming from the sandy facies, but they have a significantly higher proportion of representatives of the subclass Pteriomorphia and a lower proportion of representatives of the subclass Heterodonta (Maxwell 1988; Studencka and Studencki 1988; Studencka 1994; Dulai 1996). Carbonate sediment, generally coarse-grained, poor in organic content is the limiting factor for the infaunal burrowing suspension feeders that dominate the subclass Heterodonta and prefer a sandy bottom. This is why we examine changes in taxonomic diversity and species composition within bivalve assemblages inhabiting sandy facies and reefs.

The emphasis of this paper is on the bivalve faunas present in the Late Badenian coralline algae-vermetid reefs and in the Early Sarmatian serpulid-microbialite reefs distributed widely in the northeastern and eastern borders of the Carpathian Foredeep Basin. The study is based on published material, the collections of the Polish Academy of Sciences Museum of the Earth in Warsaw, and material obtained recently by the authors during fieldwork in 2001 and 2010.

GEOLOGICAL BACKGROUND

Middle Miocene (Upper Badenian and Lower Sarmatian) reefs are very well exposed and form hilly topography that extends about 500 km, being known as the Roztocze Hills in southeast Poland and the Medobory Hills [Polish *Miodobory*] in Ukraine and Moldova (Text-fig. 2).

In the Western Roztocze Hills, Upper Badenian algalvermetid reefs located on the northeast margin of the Carpathian Foredeep Basin are exposed in a zone 20 km long and few hundred metres wide (Bielecka 1967; Pisera 1985). The individual reef buildups stretch several hundred metres, with thicknesses reaching 10–15 m. The Lower Sarmatian serpulid-microbialite reefs occur south of the algal-vermetid reef zone. They are exposed in a zone 70 km long and few kilometres wide (Bielecka 1967; Pisera 1978). The detailed morphology of individual reefal buildups was described by Liszkowski and Muchowski (1969). The thickness of the individual reef bodies ranges from several to almost 20 metres at the Łysaków quarry (Jasionowski 1998).

The Medobory reefs separated deeper environments of the Carpathian Foredeep Basin with marls and clay deposition from the nearshore facies dominated by white quartzitic sands and sandstones, discordantly overlying the pre-Neogene basement (Maslov and Utrobin 1958). A zone a few km to 40 km wide and more than 200 km long extends from the village of Pidkamin [Polish *Podkamień*] (100 km E of Lviv) in Ukraine across the Ukrainian–Moldovan border [S of Kamianets Podilskyi (Polish *Kamieniec Podolski*)] and the Moldovan–Romanian border to the village of Ştefăneşti near the Prut river (80 km NW of Iași) in Romania.

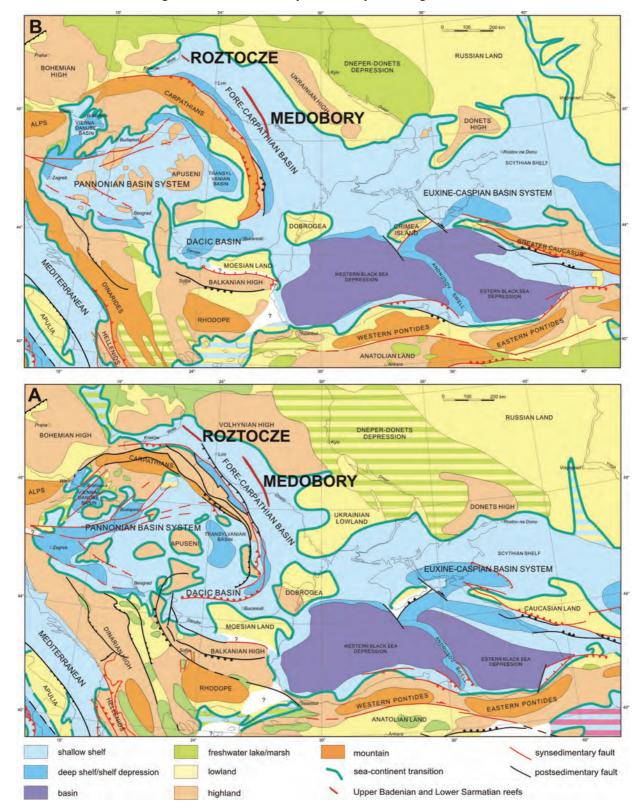
In western Ukraine, the Middle Miocene reefs form a narrow belt, 120 km long, between Pidkamin (50 km NNW of Ternopil) and Nahoriany (30 km SE of Kamianets Podilskyi), which is clearly visible in the present-day relief (Text-fig. 3).

This belt consists predominantly of Upper Badenian coralline-algae boundstones up to 100 m thick in its axial part and bioclastic grainstones and rudstones on the reef slopes (Korolyuk 1952; Janakevich 1977; Jasionowski *et al.* 2005, 2006).

Field observations have shown the presence of breccias, vadose silt and vadose leaching in the uppermost coralline-algae boundstones, indicating considerable sea-level fluctuations and a phase of emersion of the Medobory reefs in the latest Badenian.

The Lower Sarmatian (Volhynian) serpulid-microbialite reefs cover the western slopes of the Badenian coralline algae-vermetid reefs and seldom overlie their tops. They also occur at the southwest foot of the Badenian reefs forming isolated mounds up to a few tens of metres high, which are usually grouped and arranged in slightly curved linear chains that are more or less perpendicular to the Badenian reefs. The Sarmatian deposits forming these mounds (called toutra) are generally not as variable as those covering the Medobory ridge. The dominant facies is serpulid (or bryozoan) mi-

crobialite boundstone. Except for some outcrops where bivalve coquinas occur, the mounds practically lack other facies. The internal large-scale structure is usually massive, although in some places the buildups exhibit an 'onion-like' internal construction, suggesting relatively outward growth from a central core.



The Upper Badenian deposits associated with the reefs comprise a variety of bioclastic, marly and rhodoid facies while the Lower Sarmatian deposits comprise bivalve coquinas, bioclastic or oolitic grainstones, marls or clays, breccias and conglomerates. Both the reefal and surrounding deposits have been studied extensively by Laskarew (1914), Korolyuk (1952), Maslov and Utrobin (1958), Krach (1962), Kudrin (1966), Bielecka (1967), Jakubowski and Musiał (1977, 1979a, 1979b), Musiał (1987), Pisera (1978, 1985, 1995, 1996), Jasionowski (1996, 2006), Jasionowski *et al.* (2003, 2005, 2006) and Wysocka *et al.* (2007).

MATERIAL AND PROVENANCES

Although detailed geological investigations of the Miocene reefs in Ukraine began during the last decades of the 19th century (Hilber 1882a; Teisseyre 1884, 1895, 1900) and they have since been the subject of numerous studies (Laskarew 1914; Korolyuk 1952; Maslov 1956, 1962; Maslov and Utrobin 1958; Kudrin 1966), no taxonomic study of their molluscan fauna has ever been undertaken. A preliminary list of the bivalve fauna was provided by Teisseyre (1895) and Korolyuk (1952), supplemented with a few species mostly from the Staryi Zbarazh [Polish Zbaraż Stary] quarry included by Friedberg (1934–1936) and by Nevesskaja et al. (1993) in their monographs on Miocene bivalves. Only the publications of Voloshina (1973) and Janakevich (1977, 1993) attempted a systematic account of the Late Badenian bivalves from the coralline algae-vermetid reefs in Moldova.

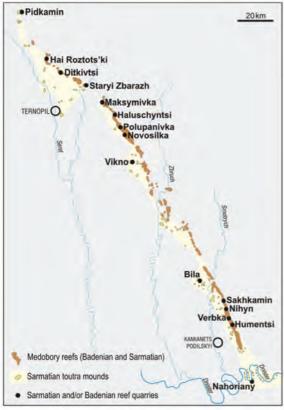
Far more is known about the molluscan fauna that existed in the coralline algae-vermetid reefs in Poland (Krach 1962, 1981; Pisera 1985; Studencka 1994). Since the bivalve fauna of the Medobory reefs remains relatively poorly known, the Late Badenian bivalve fauna from reefal facies referred to in this paper has been predominantly analysed on the basis of assemblages from the Roztocze reefs because these rich bivalve assemblages are more completely preserved in carbonate deposits, with their aragonitic shells still retained in the rock.

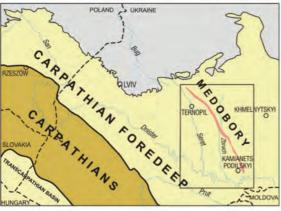
The Sarmatian serpulid-microbialite reefs in Ukraine have been intensively studied recently (Jasionowski et al. 2002, 2003, 2006; Studencka and Jasionowski 2004, 2007; Jasionowski 2006) and an extensive bivalve collection was accumulated by the present authors during fieldwork between 2001 and 2010. Studies were concentrated on the best exposed reefs and the bivalve material was collected mainly from the Hai Roztots'ki [Polish Gaje Roztockie], Ditkivtsi [Polish Dytkowce], Haluschyntsi [Polish Haluszyńce], Humentsi [Polish Humieńce], Maksymivka [Polish Maksymówka], Nihyn [Polish Niegin], Novosilka [Polish Nowosiółka Skałacka], Polupanivka [Polish Połupanówka] and Verbka [Polish Werbka] active quarries and from the abandoned Vikno [Polish Okno] quarry (Text-fig 3). The bivalve fauna is characterized by a relatively high frequency of species belonging to the subfamily Lymnocardiinae. The taxonomic study of the Lymnocardiinae was undertaken by the senior author and will be the subject of a separate publication. In addition to our material, supplementary information on Sarmatian bivalves was obtained from the collection of N.P. Paramonova kept at the Paleontological Institute, Russian Academy of Sciences in Moscow.

The analysis of the bivalve faunas of the Badenian reef limestones and sandy facies in Poland revealed that the taxonomic structure (expressed as percentages of particular subclasses of the Bivalvia according to Newell's arrangement) may depend not only on water depth, as stated by Hickman (1974), but also on sediment composition (Studencka and Studencki 1988; Studencka 1994). The changes in taxonomic diversity within Middle Miocene bivalve assemblages inhabiting sandy facies are well documented in both Central and Eastern Paratethys. The current state of knowledge of the bivalve faunas is based on taxonomically revised data presented by Studencka et al. (1998) for both the Late Badenian and Konkian assemblages, and on data documented by Krach (1938, 1967), Kojumdgieva (1969, 1976), Grischkevitsch (1970), Iljina et al. (1978), Merklin and Nevesskaja (1955), Muskhelishvili (1980), Studencka and Studencki (1980) Nevesskaja et al. (1986, 1993) and Paramonova (1986,

Text-fig. 2. Palaeogeographic maps of the Paratethyan region with location of the Roztocze and Medobory Middle Miocene reefs; modified and simplified after Popov *et al.* (2004): **A** – After the Middle Badenian (Wielician) salinity crisis, the Late Badenian transgression from the Mediterranean flooded the Central Paratethys for the last time. The coralline algal-vermetid reefs from the Roztocze and Medobory hills give evidence for the last marine invasion into southeastern Poland and western Ukraine. In the latest Badenian, with the tectonic movement of the Moldavian (Late-Styrian) Tectonic Phase of the Alpine orogeny, this marine connection with the Mediterranean was interrupted; **B** – Since the Early Sarmatian the Paratethys changed to a mixo-mesohaline (semi-marine) basin incidentally connected with the Mediterranean. The narrow marine connection and the river inflow into the huge west-east oriented Paratethys decreased water salinity leading to oversaturation in calcium carbonate. The serpulid-microbialite reefs from Roztocze and Medobory originated in this peculiar hydrochemical regime. Contemporaneously with the Early Sarmatian transgression (large areas of both the present-day Ukrainian and Russian territories were flooded) some reorganization of the palaeogeography occurred. From the Kiscellian to the latest Badenian the Carpathian Foredeep Basin formed part of the Central Paratethys. From the Early Sarmatian they were incorporated into the Eastern Paratethys realm. Connection with the Pannonian Basin System was reduced to a narrow seaway that existed until the middle Bessarabian

1994, 1995) for the Early Sarmatian (Volhynian) assemblages. Supplementary information was derived from the collection of K. Kowalewski housed in the Polish Academy of Sciences Museum of the Earth in Warsaw, the collection of W. Friedberg deposited in the Institute of Geological Sciences, Polish Academy of Sciences, Krakow and the collection of R.L. Merklin kept at the Paleontological Institute, Russian Academy of Sciences in Moscow.



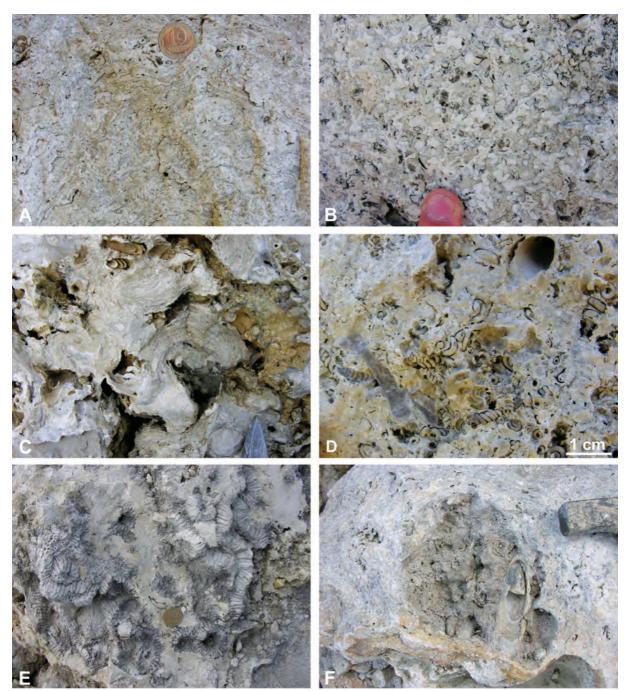


Text-fig. 3. Location and distribution of the Badenian and Sarmatian reefs of the Medobory Hills (after Korolyuk 1952; modified) and the distribution map of the Middle Miocene deposits in the Carpathian Foredeep Basin in Poland and Ukraine

CORALLINE ALGAE-VERMETID REEFS AND REEF-ASSOCIATED BIOTA

The main frame-builders of the Late Badenian reefs in both the Roztocze and Medobory hills are coralline algae which display different growth morphologies, ranging from laminar crusts to erect branching forms (Text-figs 4A, 4B). Their taxonomic composition in the Medobory reefs was studied by Maslov (1962). As demonstrated by Pisera (1985), they show most species in common with the Roztocze algal-vermetid reefs, where crustose coralline algae can constitute up to 70% of rock volume. Bryozoans are also of great importance (Text-fig. 4C). Common are representatives of the genus Schizoporella Hincks, which occur both as contributors to the reef framework and as encrustations of cavity walls. Encrusting foraminifers of the genus Nubecularia Defrance and irregular shells of the sessile vermetid gastropod Petaloconchus intortus (Lamarck) are also ubiquitous, although their abundances vary from reef to reef (Text-fig. 4D). A significant component of the reef-core facies in the Medobory reefs are hermatypic corals but these do not constitute the reef framework (Dembińska-Różkowska 1932; Korolyuk 1952; Voloshina 1973; Janakevitch 1977; Jasionowski et al. 2005) (Text-figs 4E, 4F). The coral faunas are of low diversity and dominated by two species: Tarbellastraea reussiana (Milne Edwards and Haime) and Porites vindobonarum prima (Kühn), whereas Siderastraea cf. italica (Defrance) and ?Montastraea sp. are extremely rare (Jasionowski et al. 2005, 2006). On the other hand, hermatypic corals are absent and solitary corals very scarce in the Roztocze reefs, with only a few small specimens having been documented by Pisera (1985).

The Badenian reefs of the Roztocze Hills, which developed on elevations of the sea bottom in extremely shallow water, high-energy conditions, were inhabited by a moderately diverse molluscan community (Krach 1962, 1981; Macioszczyk 1988; Pisera 1985; Studencka 1994). Brachiopods are locally common and represented by eight species. Their abundance and distribution among different facies and localities has been studied by Bitner (1990) and Baumiller and Bitner (2004). Decapod crab remains comprise 17 species belonging to 16 genera. They are mostly disarticulated and often broken but are in many cases extremely well preserved (Müller 1996). According to Pisera (1985), two ecological assemblages associated with these algal-vermetid reefs can be defined that differ in their structure and relationship to the reef body, viz., the reef assemblage and the epi-reef assemblage. The latter assemblage consists of 14 bivalve species and about 30 gastropod species, whereas in the reef assemblage 41 bivalve species and about 64 gastropod species occur. Epifaunal bivalve and gastropod elements form about threequarters of the molluscan fauna. Of these, species cementing to the substrate are the commonest and amount to almost 42% of the molluscan fauna while epifaunal bivalves that are byssally attached constitute almost one quarter. In both reef and epi-reef assemblages the dominant molluscan element is the bivalve species *Neopycnodonte navicularis* (Brocchi), occurring in small clusters (Pisera 1985). Dense overgrowths of this



Text-fig. 4. Badenian coralline algae-vermetid reefs of the Medobory Hills: **A** and **B** – Coralline algae reef framework with coralline thalli exhibiting laminar (A) and branching (B) growth pattern, Nihyn; **C** – Multilamellar colony of unidentified bryozoan growing on oyster shells, Hai Roztots'ki; **D** – Coralline algae framework with numerous spiral tiny vermetid gastropods (preserved as moulds, original shells dissolved); in the upper right - *Lithophaga* boring, Nihyn; **E** – Colony of the hermatypic coral *Tarbellastraea* sp., Nihyn; **F** – Small massive coral colony of *Porites* sp. with large *Lithophaga* boring, embedded within coralline algae framework, Sakhkamin'

species constituted the primary frame builder of oyster buildups located ca 5 km south of the algal-vermetid reef zone (Bielecka 1967; Pisera 1978; Studencka *et al.* 2005).

Systematic studies of the Medobory reef-associated biota are far from complete though some preliminary reports are available (Korolyuk 1952; Szörényi 1953; Kudrin 1966; Voloshina 1973; Janakevich 1977; Jasionowski et al. 2005; Górka and Jasionowski 2006; Radwański et al. 2006). The fossil assemblage consists of molluscs, echinoids and decapods (crabs and shrimps). Molluscs are an important and dominant component. As in the case of the Roztocze reefs, representatives of the genus Haliotis Linnaeus are numerous and constitute a very characteristic element of the gastropod fauna. Of great importance, especially in the uppermost part of the reefs, are representatives of the family Fissurellidae, tentatively identified as *Diodora* sp. Other rock-dwelling gastropods are large thick-shelled representatives of the families Conidae, Strombidae and Cypraeidae. Unfortunately, the molluscan aragonitic shells are rarely preserved; gastropods and the vast majority of bivalves originally possessing such a shell are preserved as external and internal moulds. Only bivalve genera of the subclass Pteriomorphia such as Ostrea Linnaeus, Crassadoma Bernard and Lima Bruguière, having calcitic shells, are well preserved.

COMPOSITION OF THE LATE BADENIAN REEF-DWELLING BIVALVE ASSEMBLAGES

The bivalve fauna from the Roztocze Hills in Poland has been recorded and described by Krach (1962, 1981) and by Jakubowski and Musiał (1977, 1979a, 1979b). As demonstrated by Pisera (1985), *Neopycnodonte navicularis* (Brocchi) and *Musculus biformis* (Reuss) were dominant bivalve species in the molluscan assemblage inhabiting the reef during its active growth, whereas *N. navicularis*, *M. biformis*, *Crassadoma multistriata* (Poli) and *Brachidontes biali* (Cossmann and Peyrot) [the latter species was assigned to *Septifer oblitus* (Michelotti) by Pisera (1985)] have been regarded as important forms of the epi-reef assemblage, representing inhabitants of the reef surface after termination of reef growth.

Studencka and Studencki (1988) and Studencka (1994) claimed that the predominant feeding strategies and life habit preferences were responsible for the differences in the taxonomic structure between bivalve assemblages associated with both the Lower and Upper Badenian reef limestones and those inhabiting sandy bottoms in surrounding areas. Representatives of the subclass Heterodonta by virtue of their infaunal habitat

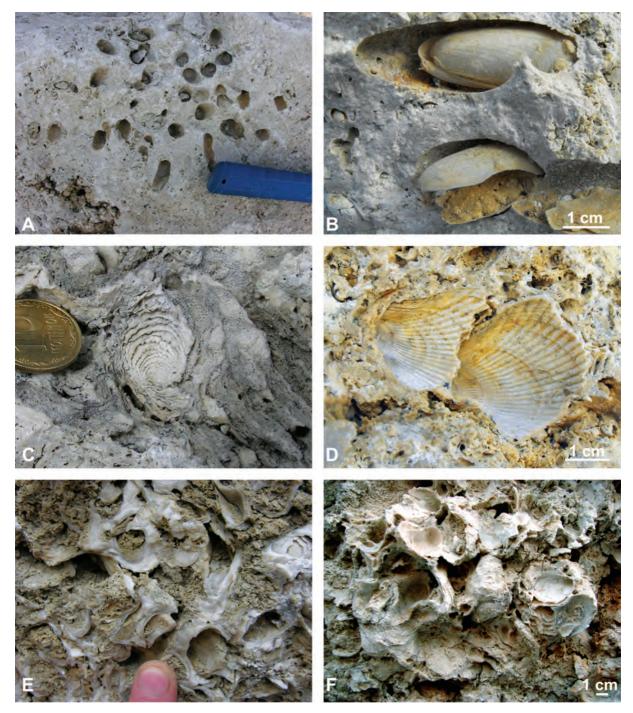
were far less common on hard substrates than on unconsolidated sediment (38-45% compared to 64-70% in sandy facies). Only those species that were capable of boring into rock or were nesters or crevice-dwellers would be represented. Representatives of the subclass Pteriomorphia, on the other hand, would usually be over-represented on hard bottoms because many of them required a firm and stable substrate (47-62% compared to 22.5% in present-day Pacific bivalve assemblages described by Hickman 1974). The Upper Badenian Roztocze reefs, originally full of caverns, provided shelter for numerous bivalves, represented mainly by typical epibenthic forms, cementing to the substrate, as well as those byssally attached. The sediment (medium to coarse-grained calcarenite with quartz grains) filling cavities and depressions within the reefs contains numerous bivalve remains. Eighty-three species are recognized (see Appendix). The most important families of the Pteriomorphia are Arcidae, Mytilidae, Limidae and Ostreidae. The pectinids are strongly dominated by Crassadoma multistriata (Poli), with sporadic Aequipecten elegans (Andrzejowski) and extremely rare other species. Of course, the specific composition is distinct in each reef (see columns 2-4 in Appendix), this being probably attributable to different depths and hydrodynamic conditions as well as to the sizes of the primary cavities that served as suitable microenvironments for numerous bivalves.

In contrast to the Roztocze coralline algae-vermetid reefs, relatively little is known of the bivalves that must have existed in the Medobory reefs. These faunas have not been studied in detail and, because of the ongoing mining operations in the quarries, no quantitative analyses were performed. However, field observations have shown that three bivalve associations may be recognized in terms of species composition: (i) *Chama (Psilopus) gryphoides-Lima (Lima) lima*, (ii) *Lithophaga* spp and (iii) *Neopycnodonte navicularis*. Because of sampling difficulties, however, no diversity data apart from species richness are available.

(i) The *Ch.* (*P.*) gryphoides-*L.* (*L.*) lima Association: This was the most diverse and commonest within the coralline algae-vermetid reefs. Usually, six to eight species are present, although as many as 12 may occur. *Ch.* (*P.*) gryphoides, a species cementing to the substrate, and the byssally attached *L.* (*L.*) lima were conspicuous elements (Text-figs 5C, 5D). Additionally, scattered specimens of *Acar clathrata* (Defrance), *Barbatia barbata* (Linnaeus), *Striarca lactea* (Linnaeus), two species of *Spondylus* Linnaeus, namely *S. gaederopus* Linnaeus and *S. crassicosta* Lamarck, and *Venus* (*Ventricoloidea*) *libella* (Rayneval, Hecke and Ponzi) contributed to this association. Pectinids were only a subordinate element

but, as in the Roztocze reefs, *Crassadoma multistriata* dominated in the association. The occurrence in the association of the probably warmer-water pectinids *Manupecten fasciculata* (Millet) and *Gigantopecten nodosi*-

formis (de Serres in Pusch) is noted (Friedberg 1934–1936; Voloshina 1973, Janakevich 1977); in Poland these species occur only in the Lower Badenian carbonates (Studencka 1999). Of great importance were



Text-fig. 5. Bivalves in the Badenian coralline algae-vermetid reefs of the Medobory Hills: A – Coralline algae reef framework with *Lithophaga* borings. Nihyn; **B** – *Lithophaga antillorum* (d'Orbigny), a common bivalve in the Nihyn quarry; **C** – external mould of *Chama (Psilopus) gryphoides* Lamarck. Nihyn; **D** – Two left valves of *Lima (Lima) lima* (Linnaeus), interior view. Nihyn; **E** – Fragment of the *Neopycnodonte navicularis* biostrome from the upper part of the Badenian reef. Hai Roztots'ki; **F** – Cluster of *Neopycnodonte navicularis* shells from the bioclastic deposits underlying coralline algae-vermetid reefs in the Humentsi quarry

gastropods (rissoids, trochids, *Conus*, *Haliotis* and *Cypraea*) but poor preservation of their predominantly aragonitic shells precluded specific identification.

(ii) The Lithophaga spp. Association: This association, especially in the uppermost part of the reefs, is overwhelmingly dominated by species typical of highenergy, rocky environments. It is represented by abundant individuals of the rock-boring bivalve genus Lithophaga Röding (Text-figs 5A, 5B). The population density was very high (more than 30 individuals/m²), with one boring adjacent to the next in some places. However, there was a distinct patchiness in the distribution of these borers, even in seemingly identical substrata in adjacent areas. Often, large limestone boulders were entirely devoid of bivalve borers, while adjacent rocks were riddled with Lithophaga spp., Gastrochaena sp. and Jouannetia semicaudata DesMoulins. Another lithophagous bivalve, Petricola rupestris (Brocchi), was also observed. The scavenger gastropod Diodora was an important element of this association.

According to Teisseyre (1895), fossils and traces of activity of at least five *Lithophaga* species are present. However, the taxonomic status of the cited specimens must be verified: in the case of many small Lithophaga traces it is difficult to decide which species is involved. Specific identification was possible only in very rare cases of Lithophaga casts and shell remains. Some of them, bearing characteristic cross-striae, can be determined as Lithophaga antillorum (d'Orbigny). The other boring bivalves, Gastrochaena sp. and J. semicaudata, were less common. Borings of these latter taxa are also commonly found in coral colonies (Radwański et al. 2006). The Lithophaga habitat presented an important biotope for numerous marine species, including the bivalve Kellia suborbicularis (Montagu), which lived in close association with the crevices of Lithophaga borings. Some individuals of the burrowing bivalve Venus (V.) tauroverrucosa (Sacco), commonly associated with rocky shore faunas, lived in gravel close by.

Similarly, studies by Korolyuk (1952) and Voloshina (1973) revealed that *Lithophaga* was by far the most ubiquitous molluscan genus in the Medobory reefs. According to Voloshina (1973), *Lithophaga* together with *Gastrochaena* and *Jouannetia* represented 37% in terms of numbers of the total bivalve population dwelling in the algal-vermetid reefs or even 90% in the case of the algal-bryozoan reefs in Moldova.

(iii) The *Neopycnodonte navicularis* Association: The species *N. navicularis* forming dense overgrowths was the primary frame builder of the oyster buildups that developed in the upper part of the coralline algae-vermetid reefs. The buildups are usually several metres

thick and are generally made of articulated, massive shells that have been filled by calcareous detritus (Text-fig. 5E). They have been observed in the Hai Roztots'ki, Ditkivtsi, Haluschyntsi and Nihyn quarries. A small oyster bank of *N. navicularis* was also noted by Teisseyre (1900) at Staryi Zbarazh. Clusters of smaller and more fragile *N. navicularis* shells are occasionally present lower in the reefs, where they occurred in association with bryozoans and serpulids (Text-fig. 5F).

These three associations are hardly comparable to those described from the Roztocze reefs.

In the two assemblages distinguished by Pisera (1985), *N. navicularis* was a dominant molluscan element in terms of biomass (about 58%), albeit in terms of frequency representing not more that 8% of the molluscan assemblage. In contrast, the occurrence of *N. navicularis* in the Medobory reefs is very scattered, except for the buildups created by comparatively bigger and more massive shells. Another very striking difference is the occurrence of boring bivalves (*Gastrochaena*, *Lithophaga*, *Jouannetia*) which were rare in the Roztocze reefs and amount to only 2.3% of the reef molluscan assemblage (Pisera 1985).

SERPULID-MICROBIALITE REEFS

The Medobory region is a key location of the Sarmatian serpulid-microbialite in western Ukraine reefs known since the 19th century (Hilber 1882b; Teisseyre 1884, 1895, 1900; Laskarew 1914; Korolyuk 1952). All the Early Sarmatian reefs in both the Roztocze and Medobory hills show a similar facies pattern. The most typical facies could be called "serpulid-microbialite boundstone" (Jasionowski 1996, 1998, 2006).

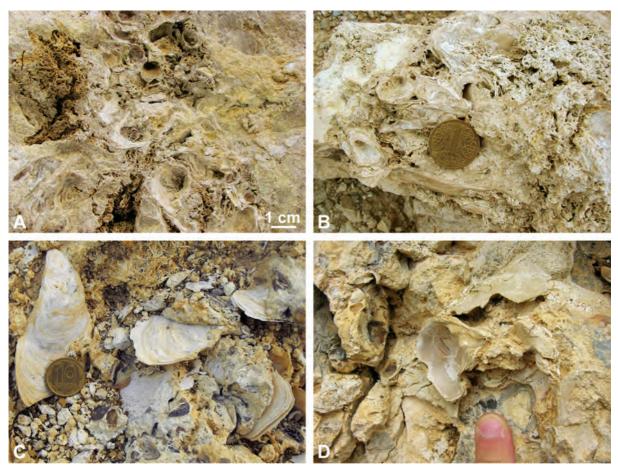
The reefs are composed of an unusual assemblage of skeletal organisms (serpulids and bryozoans) and calcite precipitates. These latter, comprising micritic and/or peloidal microbialites and synsedimentary fibrous cements, are the major reef component while serpulid tubes constitute only a few percent of the rock volume. The microbialites and the serpulid or bryozoan skeletons form together a cavernous framework that is usually filled up with abundant synsedimentary fibrous cements and micritic internal sediments. Although volumetrically subordinate, the serpulids played a key role in the reef construction. Covered by microbial mats and biofilms that mineralized and turned into peloidal microbialites, they gave rise to a lithified rigid reefal framework with widespread growth porosity that formed a space for synsedimentary cementation and internal sediment deposition. Locally, encrusting bryozoans, coralline algae and nubecularid foraminifers occur within the serpulidmicrobialite framework (Jasionowski 1996, 2006; Jasionowski et al. 2003). Encrusting bryozoans are represented mainly by the cheilostome genus Schizoporella Hincks, which typically constructs multilamellar columnar colonies up to several centimetres thick. Four other encrusting bryozoan species, Tubulipora dimidiata Reuss, Tubulipora flabellaris (Fabricius), Cryptosula terebrata (Sinzow) and Cryptosula sp., are occasionally observed but they are never abundant (Hara 2003). Titanoderma ucrainica (Maslov) is the only coralline alga to occur commonly with sessile nubecularid foraminifers (Sinzowella). Although algae are conspicuous elements incorporated into the reef framework, they are less common than bryozoans and usually form thin crusts only a few millimetres to one centimetre thick.

The absence of stenohaline marine molluscan taxa and euhaline organisms such as corals, brachiopods, decapods and echinoids in the serpulid-microbialite reefs is an inherent faunal difference between them and the coralline algae-vermetid reefs, where these groups are common. Euryhaline bivalves and gastropods are the

only faunal groups to occur commonly in the serpulidmicrobialite reefs. Gastropods are almost exclusively represented by diverse species of the rissoid genus *Mohrensternia* Stoliczka and the archaeogastropod genus *Gibbula* Risso, as well as small-sized trochids tentatively identified as belonging to the genus *Calliostoma* Swainson. Locally these are ubiquitous, whereas cerithids occur sporadically and were found within poorly sorted clastic material filling the large internal cavities and fissures.

EARLY SARMATIAN REEF-ASSOCIATED BI-VALVES

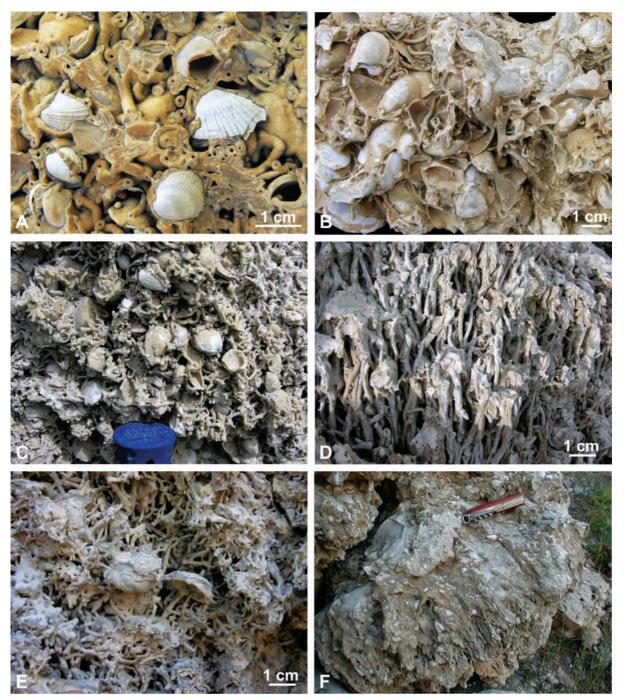
The reefs exposed along the Medobory Hills yield a significantly impoverished bivalve fauna containing only euryhaline representatives of four families. The dominant elements in decreasing order are: Cardiidae (cockles of the subfamily Lymnocardiinae), Mytilidae, Mesodesmatidae and Ostreidae. The only oyster species, *Crassostrea gryphoides* (Schlotheim), which until now



Text-fig. 6. Bivalves in the Sarmatian serpulid-microbialite reefs from the Medobory Hills: **A** and **B** – Shells of *Crassostrea gryphoides* (Schlotheim) surrounded by serpulid tubes, Humentsi; C – *Crassostrea gryphoides* (Schlotheim), Nihyn; **D** – The *Crassostrea gryphoides* bed at the Nihyn quarry

was known in the Sarmatian from sandy deposits only, is here reported for the first time from Sarmatian calcareous buildups. Two species of the genus *Ervilia* Turton represent the family Mesodesmatidae but they are extremely rare. Four mussel species are recognized *viz.*,

Mytilaster volhynicus (Eichwald), Musculus sarmaticus (Gatuev), M. gatuevi (Kolesnikov) and M. voroninae Studencka, the latter two being rare. The cockles are characterized mainly by a relatively high frequency of five species belonging to the genus Obsoletiforma Para-



Text-fig. 7. Bivalves in the Sarmatian serpulid-microbialite reefs from the Medobory Hills: **A** and **C**– Shells of *Obsoletiforma volhynica* (Grischkevitsch), surrounded by serpulid tubes, Hai Roztots'ki; **B** – *Musculus sarmaticus* (Gatuev) and *Obsoletiforma volhynica* (Grischkevitsch) with serpulid tubes and bryozoan skeletons, Polupanivka; **D** – Serpulid meadow composed of dense parallel tubes coated with microbialites, Vikno; **E** – Isolated *Obsoletiforma volhynica* shell within serpulid tubes meshwork, Vikno; **F** – Serpulid meadow composed of dense parallel tubes coated with microbialites with numerous *Obsoletiforma volhynica*, Vikno

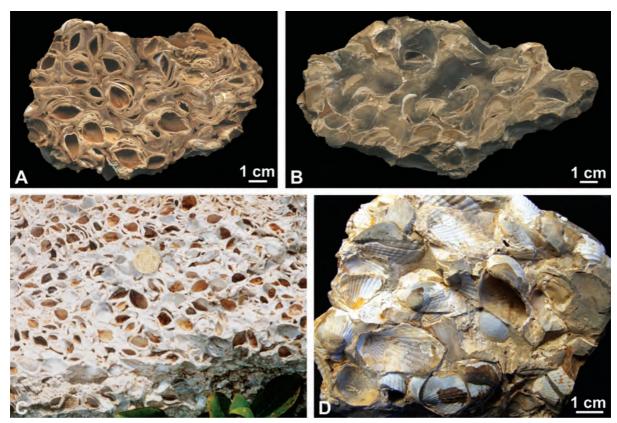
monova. No other genus of the subfamily Lymnocardiinae was found in these serpulid-microbialite buildups.

Within the serpulid-microbialite reefs four bivalve associations may be recognized in terms of species composition: (i) *Crassostrea gryphoides*, (ii) *Obsoletiforma volhynica-Mytilaster volhynicus*, (iii) *Obsoletiforma sarmatica* and (iv) *Obsoletiforma lithopodolica-Musculus sarmaticus*.

(i) The *Crassostrea gryphoides* Association: This association occurs in oyster layers in the Nyhin and Humentsi quarries (Text-fig. 6). These layers usually have a lateral extent of several tens of metres and are 20 to 50 cm thick. Shells of *C. gryphoides* dominate in the banks and frequently occur in life position. Locally the oyster species occurs in small clusters associated with serpulids. Cockles are represented only by rare *O. lithopodolica*.

(ii) The *Obsoletiforma volhynica-Mytilaster volhy-nicus* Association (Text-fig. 7): In the Vikno quarry various types of serpulid-microbialite limestone and layered bivalve coquinas are commonly observed within the reef sequence. Apart from serpulid tubes, the reef framework also consists of branching bryozoan skeletons. In places, the serpulid-microbialite limestone consists of superimposed bunches of semi-parallel serpulid tubes cov-

ered with microbialitic crusts. Shells of M. volhynicus and O. volhynica are commonly associated with these serpulid colonies. Locally, M. volhynicus greatly exceeds O. volhynica in numbers of individuals. This is the first record of the latter species in the Early Sarmatian calcareous buildups of Medobory and enables supplementary remarks concerning its intraspecific variability to be made. The shells described earlier from the sandy facies attain a maximum 15 mm in length, and are thin, delicate, subquadrate in outline and distinctly bent along the sharp edge (Grischkevitsch 1967; Nevesskaja et al. 1993). In contrast, the forms intimately associated with serpulid colonies are much longer (up to 30 mm in length), their shape having changed during the lifespan of the animal: in shells up to 12–14 mm in length the outline is subquadrate, while it is distinctly rhomboidal in larger individuals. It is highly likely that serpulid colonies provided a very favourable environment for the settlement and growth of O. volhynica. Although individuals of O. volhynica are occasionally noted in the serpulidmicrobialite boundstone exposed in all the reefs examined, this cockle species is largely restricted to this association. Apart from the Vikno quarry, this peculiar association has been observed in the Hai Rostots'ki,



Text-fig. 8. Bivalves in the Sarmatian serpulid-microbialite reefs from the Medobory Hills: **A** and **C** – Coquina of *Obsoletiforma lithopodolica* (du Bois) from the Hai Roztots'ki quarry cemented with aragonite; **B** and **D** – Coquina of gigantic shells of *Obsoletiforma sarmatica* (Kolesnikov) from the Haluschyntsi quarry; shells preserved as thin aragonitic coverings embedded within calcareous muddy matrix

Humentsi, Nihyn and Verbka quarries, and wherever the environmental conditions were sufficient to allow the growth of densely clotted serpulid colonies providing shelter for byssally attached bivalves.

(iii) The *Obsoletiforma sarmatica* Association: The species *O. sarmatica* (Kolesnikov) had a patchy occurrence, and often formed an oligotypic association in which other bivalves were scarce or absent (Text-figs 8B, 8D). Layered coquinas cover the flanks of the serpulid-microbialite reefs. Aragonitic bivalve shells are either cemented with fibrous cement or embedded in a micritic matrix. Large shells of *O. sarmatica*, about 45 mm in maximum dimensions, were observed in the Haluschyntsi quarry.

(iv) The Obsoletiforma lithopodolica-Musculus sarmaticus Association: This was the most diverse and commonest association within the serpulid-microbialite reefs. Usually three species are present viz., O. lithopodolica (du Bois), O. gatuevi (Kolesnikov) and Musculus sarmaticus (Gatuev), although as many as 10 species may occur. They include Mytilaster volhynicus (Eichwald), Musculus gatuevi (Kolesnikov), M. voroninae Studencka, O. sarmatica, O. vindobonensis (Laskarew) and O. gatuevi, which are nowhere common. Locally, shells of O. gatuevi or O. lithopodolica can form oligotypic accumulations. Coquinas are usually some decimetres in thickness and are generally made of articulated closed shells which are either empty or filled by fibrous cement. Moreover, the cavities between shells are also filled by fibrous cement (Text-figs 8A, 8C). This kind of accumulation of Obsoletiforma shells was also reported by Teisseyre (1900) from the Toutra Hill near Skalat. The occurrence of small-sized shells of Ervilia podolica (Eichwald) and E. trigonula Sokolov is documented only at the Polupanivka quarry.

Although the serpulid-microbialite reefs that occur in the Roztocze Hills maintain essentially the same biotic components as those in the Medobory Hills, their bivalve species richness is less. Apart from two species of the genus *Obsoletiforma*, namely *O. lithopodolica* and *O. gatuevi*, only four mussel species occur. So far as we know, no oyster shells have been documented.

FAUNAL CHANGES ACROSS THE BADENIAN/ SARMATIAN BOUNDARY

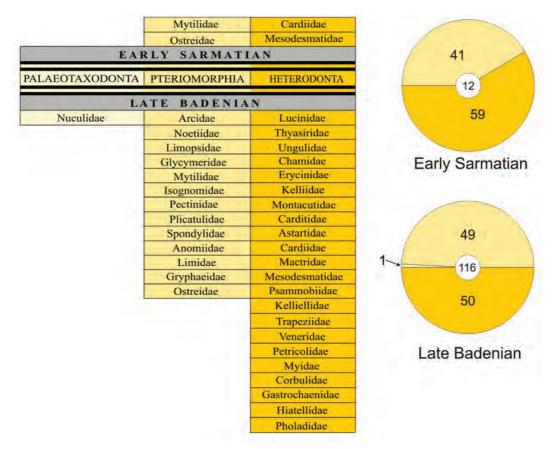
The Late Badenian transgression in the northernmost part of the Central Paratethys led to the establishment of shallow marine conditions that allowed growth of coralline algae-vermetid reefs (Korolyuk 1952; Pisera 1985, 1996; Studencki 1999). As demonstrated by Kováč *et al.* (2007), the Late Badenian sea-level fall co-

incided with the appearance of stress factors such as stratification of the water column and hypoxic conditions at the basin bottom throughout Central Paratethys. The terminal Badenian was characterized by regression that led to shallowing and to local emersions. Strong erosion marks the Badenian/Sarmatian boundary over large areas of the Pannonian Basin System (see Kojumdgieva 1969; Kováč *et al.* 2007; Rögl *et al.* 2008; Cornée *et al.* 2009) as well as in marginal parts of the Carpathian Foredeep Basin (Grischkevitsch 1970; Musiał 1987; Andreyeva-Grigorovich *et al.* 1997). Due to this abrupt environmental change the coralline algaevermetid reefs died and animals like brachiopods, corals, crabs and marine stenohaline molluscs became extinct in the Paratethys.

At the beginning of the Sarmatian the serpulid-microbialite reefs developed, made up of an unusual assemblage of skeletal organisms (serpulids and bryozoans) and microbialites (Korolyuk 1952; Liszkowski and Muchowski 1969; Pisera 1978, 1995; Musiał 1987 and Jasionowski 1998, 2006).

Hence, as a result of a drastic change in environmental factors affecting the main reef-builder organisms, the Late Badenian reef-dwelling bivalve faunas were strikingly different from those inhabiting the Early Sarmatian reefs (Text-fig. 9). The low diversity of the Sarmatian bivalve fauna, comprising only 12 species of five genera belonging to four families, contrasts sharply with the diverse assemblages documented in the coralline algae-vermetid reefs. Out the total of 116 species representing 84 genera belonging to 36 families that inhabited the Late Badenian reefs (see Appendix), only three species are known to have survived into the Sarmatian viz., M. volhynicus, C. gryphoides and O. vindobonensis. The latter species is very rare in both the coralline algae-vermetid Roztocze reefs and the serpulid-microbialite Medobory reefs. In contrast, the abundance of M. volhynicus greatly increased in the Early Sarmatian compared to its occurrence in the Late Badenian reefs. According to Korolyuk (1952), small clusters of large and thick shells of C. gryphoides occur scattered within the coralline algae-vermetid Medobory reefs. Shells of its Sarmatian descendant, distinguished as C. gryphoides sarmatica (Fuchs), are comparatively smaller and thinner.

The most noticeable difference, however, is the complete lack of marine stenohaline taxa in the Sarmatian reefs and the abundance and ubiquity of representatives of the genus *Obsoletiforma*. These were apparently characterized by the very high fertility typical of opportunists that rapidly colonize new habitats. They first occurred in the Early Badenian of the northern part of the Central Paratethys and their dispersal during



Text-fig. 9. The closure of the Mediterranean seaways was marked by an abrupt change in the taxonomic diversity of the bivalve faunas. In contrast to the Late Badenian coralline algae-vermetid reefs providing sites of attachment and inhabitation for representatives of the 37 families, the Sarmatian serpulid-microbialite reefs were inhabited only by representatives of the 4 families. Circles indicate percentage ratio of major taxonomic bivalve groups of the Badenian and Sarmatian reefs; with the number of species in the centre

the Late Badenian led to their arrival in the Eastern Paratethys (Studencka et al. 1998; Popov et al. 2005). However, in both the Late Badenian and Konkian the genus Obsoletiforma is known to be only a subordinate element represented by three species viz., O. kokkupica (Andrussow), O. lithopodolica (du Bois) and O. vindobonesis (Laskarew) (Laskarew 1903; Kojumdgieva 1969, 1976; Bałuk 1970; Kókay 1985; Nevesskaja et al. 1986, 2001, 2006 and Studencka 1986, 1999). In contrast, the genus is one of the most important elements in the Early Sarmatian fauna, being represented by 15 species (see Kojumdgieva 1969, 1987; Grischkevitsch 1970; Paramonova 1986,1994; Nevesskaja et al. 1993, 2001) which managed to live on soft bottoms (sands and clay) and within serpulid-microbialite reefs. In the reefs Obsoletiforma commonly occurred as nearly monospecific autochthonous assemblages. The fact that O. sarmatica and O. volhynica reach their largest size in nearly monotypic associations suggests that the genus was fully adapted to life in extremely stressed environments that were unsuitable for other molluscs.

ENVIRONMENTAL MODEL OF THE SARMATIAN REEFS

Large-scale reefs composed of serpulids and microbialites, such as observed in the Carpathian Foredeep Basin in the Roztocze and Medobory Hills (Korolyuk 1952; Jasionowski et al. 2003; Jasionowski 2006), Moldova (Saulea 1946) as well as in eastern Romania (Saint Martin and Pestrea 1999), are unique in the fossil record. Indeed, occurrences of small lenses and metrethick dome-shaped buildups were documented in the Upper Sarmatian s.s. of the Austrian and Hungarian parts of the Pannonian Basin System, e.g. the Styrian Basin (Friebe 1994), and of the Zsámbék Basin (Cornée et al. 2009). Similar bioconstructions were recognized within contemporaneous lower Bessarabian strata [lower Middle Sarmatian s.l.] of the Euxine-Caspian Basin System in the Kerch Peninsula (Ukraine) and the Taman Peninsula (Russia) (Goncharova and Rostovtseva 2009). In all these Middle Sarmatian bioconstructions, however, microbialites and coralline algae constitute a minor component, while the greater part of the framework is made by bryozoans and serpulids (Friebe 1994; Cornée *et al.* 2009; Goncharova and Rostovtseva 2009).

Thus, exact analogues of the serpulid-microbialite reefs are unknown from other basins and/or ages. Similar serpulid-microbialite constructions are extremely rare in the geological record: the only known examples are Triassic serpulid-microbialite buildups in the western part of the Tethys shelf in Spain and Italy (Braga and Lopez-Lopez 1989; Berra and Jadoul 1996 and Cirilli *et al.* 1999 respectively). They are supposed to have originated in ecologically extremely-stressed environments related to low oxygen concentrations in the sea water, anomalous salinities (mainly mixo-mesohaline) and eutrophic conditions.

Serpulids that encrust lithified stromatolites are also known in some Holocene/Recent saline lakes in Australia (Bone and Wass 1990) and lagoons in Tunisia (Davaud et al. 1994). Serpulids are enormously opportunistic organisms that are able to survive in environmental conditions characterized by a wide range of physicochemical parameters such as temperature or salinity (ten Hove and van den Hurk 1993). In most modern and ancient normal-marine environments serpulids, although present, play an insignificant role. Massive accumulations of serpulid tubes are typical of environments of high ecological stress that are inhospitable to other biota. The initial development of serpulid reefs generally requires firm substrates. They thrive on shallow sea bottoms, in waters with high, low or fluctuating salinities, and variable temperatures.

The key factors that explain their massive development in the Early Sarmatian are the mass occurrence of the calcite precipitates including microbialites and synsedimentary cements building serpulid-microbialite reefs, and the thick (about 7-10 m) sequence of oolitic limestones common in the nearshore parts of the basin. The presence of carbonate precipitates itself clearly indicates water highly supersaturated with respect to calcium carbonate (Pisera 1996; Jasionowski 2006) and sharply distinguishes, along with other factors such as biota, the Early Sarmatian reefs from the Badenian ones. Based on oxygen stable isotope signatures, Jasionowski (2006) hypothesized that the supersaturation was caused by strong evaporation of the mixo-polyhaline water in the marginal, shallow parts of the Early Sarmatian Sea. The δ¹⁸O values measured in the Sarmatian reef precipitates reach up to nearly +3% PDB (average +1.6%; see Jasionowski 2006) which means water δ^{18} O values as high as ca +2% SMOW (assuming temperatures of 15°-20° C) and seem to be completely incompatible with mixo-polyhaline salinity arising from simple mixing of marine and meteoric end-members.

In fact, however, such a heavy oxygen isotope composition of water is not at all at variance with mixo-polyhaline salinity. The oxygen isotope composition of water depends on the evaporation rate and not on its initial salinity. In other words, it means that the isotopic composition of water (and minerals crystallized from it) is not a direct indicator of salinity (e.g. Swart et al. 1989; Matyas et al. 1996). It is possible to obtain water of identical isotopic composition by evaporating water samples of entirely different original salinities (e.g. freshwater, mixo-polyhaline and euhaline ones). One can also obtain isotopically heavy water still with mixo-polyhaline salinity, similar to the inferred Sarmatian one, by means of evaporation of only slightly less saline water, e.g. evaporating water with initial salinity 20% and $\delta^{18}O$ as high as ca -3% SMOW to the δ^{18} O value equal + 2%SMOW increases salinity to only about 28% (for details see Jasionowski 2006, p. 452). Such a mechanism could have obtained in the nearshore parts of the Sarmatian Paratethys basin. It is probable that locally the water could even have reached hyperhaline salinity, as suggested by Pisera (1996). The ecological requirements of benthic foraminifers sampled from near-reef deposits support this interpretation. Peryt (2003) found low-diversity foraminiferal assemblages in the Hai Roztots'ki, Polupanivka and Verbka sections. The Polupanivka section assemblages are almost entirely composed of keeled elphidiids, typical opportunistic, mostly herbivorous epifaunal dwellers occurring in shallow environments of normal marine to elevated salinities (35-70%). Similar ecological requirements are characteristic of Varidentella reussi (d'Orbigny), Quinqueloculina hauerina d'Orbigny and Cycloforina predkarpatica (Serova), these being common constituents of the assemblages recorded from the Hai Roztots'ki and Verbka sections. Additional common species in these assemblages are non-keeled elphidiids. According to Murray (1991), extant species of non-keeled elphidiids are highly salinitytolerant, occurring in shallow environments in freshwater, brackish, euhaline and hypersaline (up to 70‰) conditions.

In any case, evaporation of the mixo-polyhaline Sarmatian water accounted for locally more stressed (than average-Sarmatian) environmental conditions and led to a stronger decrease in the taxonomic richness of the biota in the reefs compared to other Sarmatian facies.

However, evaporation itself seems to be insufficient to explain the pervasiveness of carbonate precipitation in the Sarmatian reefs. Pisera (1996) has suggested that the Sarmatian reefs could have originated in water with high carbonate alkalinity. Indeed, an increase in the carbonate alkalinity content in surface water is typical of stratified anoxic basins such as the present-day Black

Sea (Kempe 1990; Hiscock and Millero 2006). The bottom anoxic water in such basins is highly enriched in dissolved inorganic carbon (DIC) due to anaerobic bacterial mineralization of organic matter. Export of the carbonate alkalinity to the surface water could eventually increase supersaturation with respect to calcium carbonate (Kempe 1990), especially if coupled with evaporation. For example, the surface water of the present-day Black Sea, the largest anoxic density stratified basin today, is quite supersaturated with respect to calcium carbonate (saturation state as high as 7.5 of calcite and 4.5 of aragonite; see Hiscock and Millero 2006) and, according to Kempe and Kaźmierczak (1994), its evaporation could increase the supersaturation much more and cause rapid precipitation of calcium carbonate. Deepwater deposits that originated in bottom anoxic conditions are known from the Carpathian Foredeep Basin in Poland (Czapowski 1994; Gąsiewicz et al. 2004) so such a mechanism could also have applied to the Early Sarmatian Sea. In addition, the abundance of monotypic occurrences of the bivalve Abra (Syndosmya) reflexa (Eichwald) in deep-water deposits suggest that the oxygen level at the bottom of the whole Paratethys was never enough to make possible the settlement of a more diversified benthic biota.

Increased alkalinity in the Sarmatian Sea is also supported by the microbialite microfacies. According to Arp *et al.* (2001), the microbialite fabrics are controlled by water chemistry, specifically its alkalinity. Microbialites exhibiting clotted fabrics, such as the Sarmatian ones, originate in water with elevated carbonate alkalinity and a relative depletion in calcium. On the other hand, microbialites with calcified remnants of cyanobacteria (such as filaments) are typical of hard waters i.e. water with higher concentrations of calcium ion (Arp *et al.* 2001).

Other atypical features of the Sarmatian reefs are peculiar Mg and Sr concentrations in the calcite precipitates (Jasionowski 2006), which are entirely different from those in the petrographically similar recent equivalents (see e.g. Carpenter and Lohmann 1992). Both the microbialites and synsedimentary cements in the Sarmatian reefs are composed of medium-Mg calcite (5-6% mole CaCO₃) with a very high admixture of strontium (usually 1000-1500 ppm). As the Paratethys was connected to the Mediterranean in the Early Sarmatian (Paramonova 1995; Iljina 1998, 2000; Steinninger and Wessely 2000; Popov et al. 2004), the ionic composition of its water had to be marine and more or less similar in composition to that of modern marine water (Holland 2003). Consequently, the chemical composition of the Early Sarmatian water could not have been responsible for the peculiar geochemistry of the calcitic precipitates in the Sarmatian reefs. An alternative explanation is that a very high precipitation rate in the highly super-saturated water caused a preferential uptake of Sr ions into calcite crystals (see more in Jasionowski 2006).

Summarizing, the mass occurrence of serpulids in the Early Sarmatian was possibly attributable to very peculiar environmental conditions characterized by highly alkaline and calcium carbonate-supersaturated water, the latter feature resulting from strong evaporation. The establishment of such conditions was due to restricted connections of the Paratethys to the world ocean at the onset of the earliest Sarmatian. This led to a freshening of the whole water body of the basin, then possibly to its density stratification and an alkalinity build-up in anoxic bottom water that was exported to the surface, and eventually to evaporation of the water in the nearshore environments.

THE BADENIAN/SARMATIAN EXTINCTION EVENT: RESPONSE OF INHABITANTS OF SANDY BOTTOMS

Reef-associated bivalves versus bivalves populating sandy bottoms

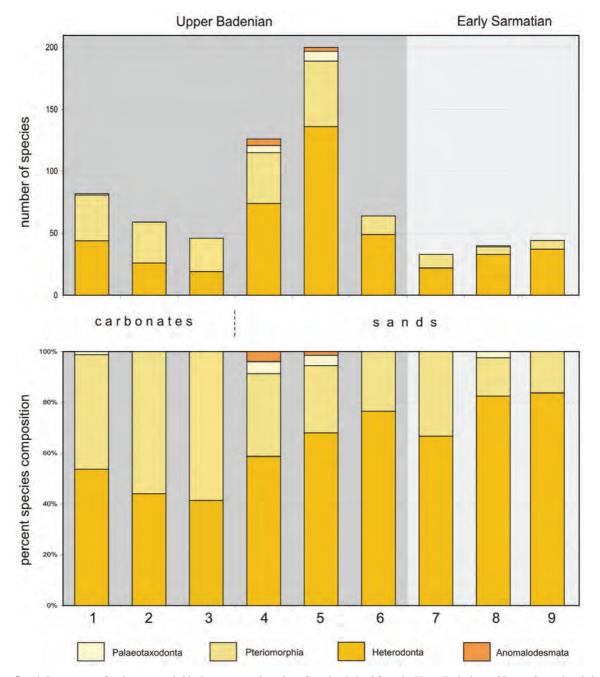
Bivalves are a valuable tool for palaeobiogeographic purposes because they occupy a wide range of ecological niches and have a sensitive reaction to all environmental parameters. As shown in the chapter "Faunal changes across the Badenian/Sarmatian boundary", the taxonomic diversity of bivalves dwelling in the Late Badenian coralline algae-vermetid reefs underwent severe reduction (see Text-fig. 9) due to the restricted connection of the Paratethys to the Mediterranean. Out of 116 bivalve species documented in the coralline algae-vermetid reefs, 113 had their last occurrences in the Paratethys. Only three species (i.e. 2%) occur in both the coralline algae-vermetid and serpulid-microbialite reefs.

By far the most diversified Late Badenian bivalve fauna has been recorded in the sandy facies of areas adjoining the Medobory reefs. Out of 200 bivalve species reported from the Upper Badenian sandy facies of the Volhynian and Podolian areas (Friedberg 1934–1936; Nevesskaja *et al.* 1993; Studencka *et al.* 1998), 23 species (i.e. about 12%) were also noted in Early Sarmatian assemblages (Krach 1938; Grischkevitsch 1970; Kulchytsky and Kulchytsky 1983; Nevesskaja *et al.* 1993; Paramonova 1994 and our study); they are dominated by representatives of the subclass Heterodonta. The bivalve diversity was reduced due to the Badenian/Sarmatian extinction event, albeit not as severely as in the Upper Badenian reefs.

Therefore, Badenian and Sarmatian bivalve assemblages from reefs and sands can be contrasted in two ways (Text-fig. 10): (i) the diversity of the sandy facies faunas was higher than that of the reef faunas and (ii) the

proportion of Heterodonta was higher in the sandy assemblages than in the reefal assemblages (68–77% and 41–45% respectively).

The above remarks form a basis for further analysis



Text-fig. 10. Percentages of major taxonomic bivalve groups and number of species derived from the Upper Badenian and Lower Sarmatian shallow-marine deposits of: 1 – the Roztocze reefs, Poland (data based on Krach 1981; Studencka 1994; Chwiluk 2004); 2 – the Medobory reefs, Ukraine (data based on Teisseyre 1900; Friedberg 1934–1936; Korolyuk 1952 and our study); 3 – the Medobory reefs, Moldova (data based on Voloshina 1973; Janakevich 1977, 1979); 4 – south-eastern Poland (data based on Krach 1967; Jakubowski and Musiał 1977, 1979a, 1979b; Studencka *et al.* 1998); 5 – Volhynian and Podolian areas, Ukraine (data based on Friedberg 1934–1936; Studencka *et al.* 1998); 6 – Moldova (data based on Voloshina 1973; Studencka *et al.* 1998); 7 – southern slopes of the Holy Cross Mts., Poland (data based on Krach 1967; Czapowski and Studencka 1990); 8 – Volhynian and Podolian areas, Ukraine (data based on Krach 1938; Kulchytsky and Kulchytsky 1983; Nevesskaja *et al.* 1993; Paramonova 1994 and our study); 9 – Moldova (data based on Kolesnikov 1935; Simionescu and Barbu, 1940; Nevesskaja *et al.* 1993)

of the bivalve fauna from the sandy facies, in order to evaluate how this group reflected the temporary closure of seaways between the Paratethys and the Mediterranean area around 13.3 Ma.

Changes within bivalve sand-dwellers across the Badenian/Sarmatian boundary

The bivalve faunas which populated shallow-water sandy bottoms of the entire Paratethys area in Late Badenian-Konkian time have been revised in detail by Studencka et al. (1998). According to these data, a centre of diversity developed in the Central Paratethys, where 316 species of 171 genera belonging to 61 families are noted. In contrast, the contemporaneous bivalve fauna which inhabited the Eastern Paratethys was less diverse and comprised 97 species of 70 genera belonging to 20 families: what is very significant is that it is dominated by immigrants from the Central Paratethys. With the disconnections of the Mediterranean seaways and reorganisation of the biogeographic patterns within the Paratethys during the latest Badenian and Konkian (Veselanian time) bivalve diversity declined drastically (Bagdasarjan 1983; Iljina et al. 1976; Kókay 1985; Muskhelishvili 1980; Nevesskaja et al. 1986, 2006; Paramonova 1994, 1995; Popov et al. 2005; Studencka 1999).

Out of the 61 families that have been recorded in the Upper Badenian sandy facies of the Central Paratethys representatives of only 20 families survived and are recognized in the Early Sarmatian fauna. In contrast, out of the 29 families that populated the Eastern Paratethys in the Konkian, representatives of 11 families are present in the Early Sarmatian from the Euxine-Caspian Basin System (Nevesskaja *et al.* 2005). However, representatives of 17 bivalve families populated vast territories of the Euxine-Caspian Basin System and the Carpathian Foredeep Basin (Text-fig. 11).

The bivalve fauna inhabiting Central Paratethys during the Late Badenian was characterized by a large number of taxa showing wide geographical distribution and strong affinities with the faunas of the northeast Atlantic and Mediterranean provinces (Studencka *et al.* 1998; Studencka 2001). In contrast, the majority of the 45 bivalve species recognized in the Early Sarmatian fauna was limited to the Paratethyan Province (Paramonova 1995). It is remarkable that the endemic forms of the latest Badenian–Konkian, being only subordinate elements in these faunas, reached their highest development in the Early Sarmatian (Volhynian). Along with the high percentage of purely Sarmatian forms, which includes 12 representatives of the subfamily Lymnocardiinae, 22 out of 40 bivalve species recorded from the

sandy facies of the western Ukraine, also occurred in the Late Badenian of the Central Paratethys (Kulchytsky and Kulchytsky 1983; Nevesskaja et al. 1993; Paramonova 1994; Studencka et al. 1998). These assemblages inhabiting shallow, well-aerated environments were dominated by Ervilia podolica (Eichwald), Loripes (Loripes) dujardini (Deshayes) and two species of the genus Plicatiforma Paramonova, namely P. praeplicata (Hilber) and P. pseudoplicata (Friedberg). Examination of the species composition of the bivalve faunas from the sandy facies of western Ukraine revealed strong affinities with other Early Sarmatian faunas from the Carpathian Foredeep and Dacian basins. With the exception of P. pseudoplicata, which first appeared in the earliest Sarmatian, all the dominant species are known to have been only a subordinate element of the Late Badenian fauna in the two basins (Laskarew 1903; Kojumdgieva 1969, 1976; Kojumdgieva and Popov 1987; Nevesskaja et al. 1986; Studencka 1986, 1999 and Paramonova 1995).

On the other hand, the bivalve faunas that inhabited the sandy bottom of the Euxine-Caspian Basin System comprised 45 species belonging to 21 genera. Of these, about 60% were new Paratethyan endemic species that originated during the Early Sarmatian (Paramonova 1995; Nevesskaja *et al.* 2005).

Thus, the separation of the Paratethyan and Mediterranean Seas resulted not only in dramatically reduced diversity of the bivalve faunas but also in the sudden evolution and dispersal of a few opportunistic species that were ancestral forms to Sarmatian species. The Early Sarmatian bivalves are dominated by endemic taxa belonging to euryhaline families, of which the Cardiidae, represented by not less than 17 species of the genera Inaaquicostata Kojumdgieva, Obsoletiforma Paramonova, Planocardium Paramonova and Plicatiforma Paramonova, reached their highest development (Nevesskaja et al. 1986, 2001, 2006; Paramonova 1986, 1994; Popov et al. 2005). As a matter of fact, the great difference in species composition between faunas of the Paratethys and those from the northeast Atlantic and Mediterranean Sea is observed. These regions have only 13 species in common: Nuculana (Jupiteria) pygmaea (Münster), Bathyarca pectunculoides (Scacchi), Pododesmus (Monia) squamulus (Gmelin), Crassostrea gryphoides (Schlotheim), Loripes (L.) dujardini (Deshayes), Loripes (Microloripes) dentatus (Defrance), Solen subfragilis Eichwald, Gastrana fragilis (Linnaeus), Gari (Gabordeus) labordei (Basterot), Abra (Syndosmya) alba (Wood), Alveinus nitidus (Reuss), Gouldia (G.) minima (Montagu) and Corbula (Varicorbula) gibba (Olivi).

Eastern Paratethys Solenidae Mactridae EARLY SARMATIAN Glycymeridae Mytilidae KONKIAN Noetiidae Anomiidae Pectinidae Pinnidae Ostreidae Nuculanidae Nuculanidae Late Badenian-Konkian Paratethys Early Sarmatian Paratethys Carpathian and Dacian basins Eastern Paratethys Central Paratethys Ton Son SARMATIAN sammobiidae Kelliiellidae LATE BADENIAN Dreissenidae **Trapeziidae** Semelidae Pholadidae Cardiidae Mactridae Central Paratethys Glycymeridae Manzenellidae Isognomonidae Arcidae Limopsidae Mytilidae EARLY Mytilidae Pinnidae Pteriidae Limopsidae Plicatulidae Spondylidae Anomiidae Pectinidae Anomiidae Ostreidae Noetiidae Arcidae Nuculanidae Nuculidae Nuculanidae

TAXONOMIC COMPOSITION OF THE EARLY SARMATIAN BIVALVE SAND-DWELLERS

Variable sedimentary conditions in the Early Sarmatian Paratethyan Sea led to the development of short-lived biocenoses, dominated by opportunistic species. They were resistant against physical stress and capable of rapid colonization of the sea bottom (Studencka and Studencki 1980; Nevesskaja et al. 1986, 2006; Czapowski and Studencka 1990; Paramonova 1994; Popov et al. 2008). Their structure was controlled mainly by external factors and the integration level was low. The degree of endemism of these assemblages is high: nearly two-thirds of all the bivalve species have not been recorded outside the Paratethyan Province. This is probably a reflection of the partially enclosed nature of the Paratethys basins, where for a long period during the Middle Miocene fully marine conditions were confined to a small Central Paratethys, while over most of the Eastern Paratethys marginal marine conditions with fluctuating or generally lower salinities prevailed (comp. Krasheninnikov et al. 2003 and references therein, Popov et al. 2005).

All the relatively diverse bivalve assemblages of the Early Sarmatian are characterized by the distinctive tripartite nature of their taxonomic composition, with regard to both origin and geographic distribution of particular species (cf. Laskarew 1903). Using the Laskarew taxonomic composition concept, Kolesnikov (1940) recognized these three groups as follows: (1) the group composed of species of Mediterranean origin; (2) the group containing Paratethyan species that originated in the Eastern Paratethys during the Konkian; and (3) the group composed of endemic species that originated in the Early Sarmatian and proliferated during the Middle Sarmatian.

Since the publication of Kolesnikov (1940) our knowledge of Sarmatian bivalves has steadily accumulated (e.g. Papp 1952, 1974; Sieber 1954; Kojumdgieva 1969, 1976; Švagrovský 1971; Iljina *et al.* 1976; Muskhelishvili 1980; Bagdasarjan 1983; Bohn-Havas 1983; Paramonova 1986, 1994, 1995 and Studencka 1990). It appears that the species constituting group 1 were widely distributed throughout the northeast Atlantic, Mediterranean and Paratethys during

the Early-Middle Miocene. Since the distribution of these species within the Sarmatian Sea provides some of the most important environmental evidence for interpreting palaeosalinity, the group is discussed in more detail in the next chapter.

Group 2 consists of both Konkian and Badenian remnants restricted to the Paratethyan Province. The majority of these species, which belonged to marine euryhaline genera such as *Musculus* Bolten in Röding, *Mytilaster* Monterosato, *Cerastoderma* Poli and *Ervilia* Turton and the subgenera *Mactra* (*Sarmatimactra*) Korobkov, *Donax* (*Paradonax*) Cossmann and Peyrot, *Donax* (*Sarmatidonax*) Bagdasarjan and *Venerupis* (*Polititapes*) Sacco, originated either in the Late Badenian Central Paratethyan Sea or in the Konkian Eastern Paratethyan Sea and became extinct during the latest Early Sarmatian, while some of them still existed during the Middle Sarmatian.

Whilst group 3 consists of endemic species that originated in the Early Sarmatian and thrived during the Middle Sarmatian, only a single endemic genus, *Planocardium* Paramonova, belonging to the subfamily Lymnocardiinae, originated during this time.

The percentage ratio of groups 1, 2 and 3, as understood here, is 32:14:56 in the Pannonian Basin System and 16:24:60 in the Euxine-Caspian Basin System (Paramonova 1986, 1994).

The percentage ratio of groups 1, 2 and 3 varied between the basins, being 30:22:48 in the northern part of the Carpathian Foredeep Basin, 23:36:41 in the Ukrainian part of the Carpathian Foredeep Basin, 9:41:50 in western Georgia and 9:38:53 in northern Ustiurt and Turkmenistan. This calculation is based on papers by Krach (1938, 1967), Merklin and Nevesskaja (1955), Kojumdgieva (1969), Mushelishvili (1980), Kulchytsky and Kulchytsky (1983), Paramonova (1986), Czapowski and Studencka (1990), Nevesskaja *et al.* (1993) and our studies.

The southeastward decrease in importance shown by group 1 (Text-fig. 12) suggests that salinity was the factor controlling the distribution of the relevant species. This interpretation is supported by the results of earlier investigations of the carbon and oxygen stable isotope contents of bivalve shells, which demonstrated aneastward decrease in salinity (Kiyashko and Paramonova 1987).

CONSIDERATIONS CONCERNING THE SALIN-ITY OF THE EARLY SARMATIAN SEA

Numerous papers have been devoted to the palaeon-tological and environmental aspects of the Early Sarmatian Sea. It was previously believed to be an isolated basin of reduced salinity: 14‰ at the beginning of the Sarmatian in the Eastern Paratethys (Iljina *et al.* 1976; Nevesskaja *et al.* 1986, 1987) and 25‰ to 18‰ within the Pannonian Basin System (Brestenská 1974).

More recently, the Early Sarmatian Paratethys was thought to have been a basin of mixo-mesohaline salinity, incidentally connected with the Mediterranean (Paramonova 1995; Iljina 2000; Popov *et al.* 2004, 2005; Nevesskaja *et al.* 2005). This generally accepted interpretation strongly contrasts with the statement by Piller and Harzhauser (2005), who postulated normal marine conditions within the entire Early Sarmatian Sea.

Therefore, the discussion on the regime of the Early Sarmatian Sea should start from the presentation of the scenario of events that took place in both the Central and Eastern parts of the Paratethys, in the Late Badenian and Konkian respectively, before the Badenian–Sarmatian Extinction Event

Earliest Late Badenian [approximately contemporaneous with the early Konkian]

At the beginning of the Late Badenian the sea invaded not only a wide area of the Carpathian foreland along the southwestern margin of the East European Platform but it also flooded the area between the present-day Dniestr and Prut rivers, allowing the establishment of a marine gateway between the Central and Eastern Paratethys (see Text-fig. 2A). As a consequence, both parts of the Paratethys were re-connected and normal marine conditions re-established in the Eastern Paratethys since the middle Tarkhanian. After the Middle Miocene (Karaganian) salinity crisis, the Eastern Paratethys could have been re-colonized by migrants from the Central Paratethys (Studencka et al. 1998; Krasheninnikov et al. 2003; Popov et al. 2005). According to the geological data (e.g. Roshka and Khubka 1981; Gontsharova and Iljina 1997; Krasheninnikov et al. 2003) this shallow Predobrogean Strait was about 150-200 km wide and enabled faunal migration into the Eastern Paratethys. This one-way migration was demonstrated by Krasheninnikov et al. (2003) on the basis of benthic foraminifers. The richness of the benthic foraminiferal assemblages decreases in general from west to east: the Upper Badenian deposits of the Podolian area (western Ukraine) yield 250 species, contemporaneous strata of southern Moldova about 170

species, whereas in the whole territory of the Euxine-Caspian Basin System only 60-70 species were found. Of the taxa found in the lower Konkian of the Eastern Paratethys, 20–22 species are assumed to have migrated from the Central Paratethys, 25–30 species are Eastern Paratethyan endemics that originated in the early Konkian, and the others were left in open nomenclature. Studies by Krasheninnikov et al. (2003) are expected to provide fundamental information on palaeoenvironmental factors in the Konkian of the Eastern Paratethys. The gateway allowed the dispersal of Late Badenian benthic foraminifers as far east as the northern Precaucasus and western Georgia. The migrants from the Central Paratethys did not include agglutinated foraminifera. Although the migrants are dominated by taxa exhibiting particularly high tolerance to environmental stress such as fluctuations in salinity, they usually secreted smaller (half or one-third) and more delicate tests than their contemporaneous Late Badenian relatives. As argued by Krasheninnikov et al. (2003), benthic foraminiferal assemblages inhabiting the Eastern Paratethys in the Konkian are thought to have been controlled largely by salinity. Correspondingly, he supposed that despite the short-lived connection between the two parts of the Paratethys during the early Konkian (Sartaganian time), free faunal exchange between the Central Paratethys and the Eastern Paratethys was equally as problematic as a broad connection of the Eastern Paratethys to the world ocean

The data on the molluscan fauna seem to confirm this conclusion. The Central Paratethys was inhabited by a diverse molluscan fauna, and both the Late Badenian bivalve (316 species) and gastropod (606 species) faunas are largely rooted in the Early Badenian (Studencka et al. 1998; Harzhauser and Piller 2007, respectively), while the Konkian molluscan fauna lacks nearly all remnants of the Chokrakian and Karaganian faunas. Out of the 97 bivalves found in the Konkian deposits there were only four remnant Karaganian species (Studencka et al. 1998), and three Chokrakian survivors were found in the Konkian gastropod fauna, which comprises 65 species (Iljina 1993). Furthermore, the molluscan records have also shown another possibility for the connection of the Eastern Paratethys to the East Mediterranean, through the presumed Middle Arkas Strait (Iljina 1994, 2000; Gontsharova and Shcherba 1997; Studencka et al. 1998).

Mid-Late Badenian [= late Konkian]

However, the Predobrogean Strait enabling faunal migration into the Eastern Paratethys during the early Konkian (Sartaganian time) was only a short-lived connection and, during the tectonic movements in the Carpathians, it became closed in the late Konkian. This closure is reflected in the extinction of the Central Paratethyan foraminiferal migrants in the Eastern Paratethys (Krasheninnikov *et al.* 2003).

A significant change is also recorded in the gastropod fauna. According to Iljina (1994), out of 65 gastropod species known from the early Konkian, 48 species occur in the late Konkian assemblages. However, and more significantly, 17 species less tolerant to salinity fluctuations vanished in the late Konkian.

There was likewise a change in the composition of the bivalve fauna: the proportion of stenohaline taxa declined markedly (ten families vanished) and, in contrast, there was an increase in the proportion of euryhaline endemic taxa. (Popov *et al.* 2005).

Furthermore, studies of the Late Badenian and Konkian representatives of the genus *Acanthocardia* Gray clearly illustrated that closure of the gateway generated large variability of the shell outline in the Eastern Paratethyan species, a weaker hinge and a reduced number of ribs (Studencka and Popov 1996).

There has been some controversy concerning the salinity of the Eastern Paratethys in the early Konkian. On the one hand, Iljina (2000) and Popov *et al.* (2004, 2005), following Merklin (1953), supposed that the euhaline salinity (between 30 and 32‰) of the Eastern Paratethys during the early Konkian (Sartaganian time) dropped to 20‰ during the late Konkian (Veselanian) due to the restricted connection to the Mediterranean. On the other hand, Kókay (1985) pointed out that: the Konkian bivalve fauna exhibited less species diversity than the one inhabiting the present-day Black Sea in that it lacked many euhaline taxa. Furthermore, the ecological requirements of the majority of the bivalve taxa suggest that the salinity of the Eastern Paratethys in the early Konkian never exceeded 25‰.

Hence, after the short-term connection, the mid-Late Badenian and late Konkian times again witnessed two separate Paratethys basins: the small but palaeogeographically differentiated Central Paratethys (encompassing the Pannonian Basin System, Carpathian Foredeep Basin and Dacian Basin), showing normal salinity, connected with the Mediterranean and inhabited by high diversity molluscan communities; and the three times larger Eastern Paratethys, with a salinity of ca 20‰, and molluscan communities strongly impoverished in numbers of species.

It appears that, simultaneously with the closure of the Predobrogean Strait, significant changes in the paleogeographic configuration occurred in individual basins within the Pannonian Basin System and the Carpathian Foredeep Basin (e.g. Czapowski 1994; Kováč et al. 2007; Roshka 2008). Tectonically induced sea-level changes led to shallowing and emerging marginal areas, and consequently were the main reason for the origin of embayments characterized by fluctuating salinity which apparently was advantageous for the development of euryhaline bivalve taxa and the origination of new species. A slight decrease in salinity in these areas, temporarily connected with open sea, might have been reflected by a remarkable decline of taxonomic richness and the flourishing of euryhaline taxa (see Laskarew 1903; Kókay 1985; Jasionowski et al. 2006). During that time, which could probably be related to the moment of appearance of Palliolum bittneri (Toula) in the uppermost part of the Flabellipecten besseri Zone, the following bivalve species originated: Obsoletiforma vindobonensis (Laskarew), Mactra (Sarmatimactra) eichwaldi Laskarew, Ervilia podolica (Eichwald), Abra (Syndosmya) reflexa (Eichwald) and Tapes (Polititapes) vitalianus (d'Orbigny). Their occurrence was detected in the Late Badenian fauna from the Polish and Ukrainian parts of the Carpathian Foredeep Basin (Bałuk 1970; Studencka 1986, and Laskarew 1903; Grischkevitsch 1970; Nevesskaja et al. 1993, respectively).

Terminal Badenian [=terminal Konkian]

Shortly afterwards, in the latest Badenian, definitive closure of the extensive seaway connecting the northeast Atlantic and Mediterranean to the Paratethys took place, following the sea-level drop throughout Paratethys (Nevesskaja et al. 1987; Popov et al. 2004, 2005; Harzhauser and Piller 2004; Kováč et al. 2007). This resulted in the predominance of meteoric water inflow over evaporation in the hydrologic balance and produced water of decreased salinity. This, in turn, brought about a dramatic change in the marine biota, which was named by Harzhauser and Piller (2007) the Badenian-Sarmatian Extinction Event. Euhaline organisms such as planktonic foraminifera, corals, brachiopods, echinoids, chitons and mostly gastropod and bivalve taxa became extinct in the Central Paratethys and never returned to the Paratethys. The bivalve fauna was strongly influenced by the closure of the Mediterranean seaways: out of the 316 bivalve species listed by Studencka et al (1998) from the Upper Badenian sandy facies of the Central Paratethys only 20 are documented in the Sarmatian fauna. As demonstrated by Harzhauser and Piller (2007), only eight out of the 606 species of gastropods recognized in the Late Badenian assemblages are represented in the Sarmatian fauna of the Pannonian Basin System. Impoverishment of the molluscan fauna in the Eastern Paratethys was also noted (Paramonova 1995; Iljina 1998, 2000; Popov et al. 2005).

This disconnection of the Paratethys from the Mediterranean marks the Badenian /Sarmatian boundary in the Central Paratethys, contemporaneous with the Konkian/Sarmatian (Volhynian) boundary in the Eastern Paratethys. A considerable hiatus at the Badenian/Sarmatian boundary indicated by strongly erosive discordance is documented in the large territory of the Pannonian Basin System (Kojumdgieva 1969; Piller and Harzhauser 2005; Harzhauser and Piller 2007; Kováč et al. 2007; Rögl et al. 2008) as well as on the northern margin of the Euxine-Caspian Basin System (Nevesskaja et al. 1987). On the other hand, continuous sedimentation between the Badenian and the Sarmatian is to be expected in the Carpathian Foredeep Basin (Czapowski 1994; Krzywiec 200; Gąsiewicz et al. 2004). Preliminary examination of the deep-water deposits from the Polish part of the Carpathian Foredeep proves, however, that the Badenian-Sarmatian transition was broadly coupled with a significant change of geochemical characteristics, especially carbon and oxygen stable isotope ratios and TOC content (Gasiewicz et al. 2004).

Early Sarmatian

At the beginning of the Sarmatian, a new narrow gateway opened from the Mediterranean towards the Paratethys (Paramonova 1995; Iljina 1998, 2000; Steininger and Wessely 2000; Popov et al. 2004). The sea invaded a large area of the Pannonian Basin System and the Carpathian foreland, as well as the Ukrainian and Russian highlands, and the shoreline shifted towards the north (see Text-fig 2B). However, the narrow marine connection and the predominance of meteoric water inflow over evaporation in the hydrological balance produced water with decreased salinity. Considering the ecological requirements of the benthic foraminifera recognized in the Lower Sarmatian of the western part of the Central Paratethys as well as the conspicuous absence of planktonic foraminifera, the salinity of the Pannonian Basin System was assumed by Brestenská (1974) to have been between 25 and 18‰. On the other hand, palaeontological analyses of the foraminifera and ostracods, coupled with carbon and oxygen stable isotope analyses of their tests from the central part of the Pannonian Basin allowed estimation of seawater salinity from 20 to 32‰, the maximum values being recorded at the end of the Elphidium reginum Zone (Tódh et al. 2010).

In addition, a peculiar environment developed in the shallow nearshore areas: the basin underwent local evaporation of the hyposaline waters, thereby giving rise to strong supersaturation with respect to calcium carbonate and consequently triggering abundant calcium

carbonate precipitation (Pisera 1995; Jasionowski *et al.* 2003; Jasionowski 2006).

This Sarmatian trangressive event was associated with tectonic movement in the Alpine-Carpathian mountain chain that resulted in important palaeogeographic changes in Paratethys and the opening of a broad connection between two Paratethys basins: the small Central Paratethys and the three times larger Eastern Paratethys, the latter showing salinity less than 20% (Popov *et al.* 2004, 2005).

It is well known that the dramatic palaeogeographical events that took place in the Paratethys have played a crucial role in the evolutionary history of several marine taxa as well as in shaping the Sarmatian biogeography and biodiversity of the regional molluscan fauna (for examples see Popov et al. 2005; Nevesskaja et al. 2006; Harzhauser and Piller 2007). During the Early Sarmatian, accelerated evolution of molluses under condition of decreased competition took place and a large number of new forms appeared suddenly (Nevesskaja et al. 2006). They originated from ancestral forms existing in the Late Badenian and Konkian, and dispersed throughout the whole Paratethys due to the broad connection between the two Paratethys basins. This brought about faunal homogeneity within the whole basin, extending from eastern Austria to Turkmenistan. It should be emphasized that no bivalve species invaded the Paratethys during the Sarmatian transgression. Therefore, the Sarmatian bivalve fauna consists predominantly of indigenous species that originated in the earliest Sarmatian and those which survived the Badenian-Sarmatian Extinction Event. These comprise both Paratethyan endemics that originated in the Late Badenian and Konkian as well as species having a wide geographic distribution in Early-Middle Miocene. The occurrence of the latter group, however, is mostly confined to the basal sandy facies belonging to the Anomalinoides dividens Zone in the Carpathian Foredeep Basin. The bivalve species viz., Nuculana (Jupiteria) pygmaea (Münster), Bathyarca pectunculoides (Scacchi), Pododesmus (Monia) squamulus (Gmelin), Alveinus nitidus (Reuss), Gouldia (G.) minima (Montagu) and Corbula (Varicorbula) gibba (Olivi) are documented only in the Polish and Ukrainian parts of the Carpathian Foredeep Basin (Studencka and Studencki 1980; Czapowski and Studencka 1990, and Kulchytsky and Kulchytsky 1983, respectively). It is notable that they did not disperse within Paratethys during the Sarmatian.

Although the bivalve fauna which survived the Badenian-Sarmatian-Extinction-Event is dominated by taxa exhibiting particularly high tolerance to environmental stress such as salinity fluctuations, some of them viz., *C. gryphoides*, *Gastrana fragilis* (Linnaeus) and *Gari* (*Gabordeus*) *labordei* (Basterot) secreted

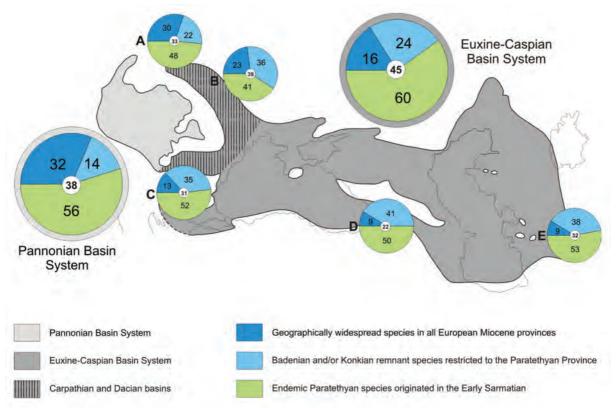
smaller and more delicate shells than their Badenian ancestors.

Summarizing, the Paratethyan bivalve fauna around the Badenian/Sarmatian boundary is characterized by a decrease in the number of families (see Text-figs 9 and 11), an impoverished generic composition and the absence of euhaline taxa. The new Sarmatian fauna became established due mainly to the radiation of the lymnocardiid genera Inaequicostata, Obsoletiforma and *Plicatiforma*. The diversity of the bivalve fauna within the Paratethys is low, comprising many species endemic to particular basins. Paramonova (1995), recognized 38 bivalve species in the Pannonian Basin System and 45 bivalve species in the Euxine-Caspian Basin System. The richness of the endemic species assemblages inhabiting soft bottoms of the early Sarmatian Sea increases in general from west to east (Text-fig. 12). As demonstrated by Merklin and Nevesskaja (1955) and by Nevesskaja et al (1995), the bivalve fauna inhabiting the eastern part of the Caspian area was dominated by species of the genus *Obsoletiforma*, while the group of species having wide geographic distribution in the

Early-Middle Miocene is represented only by *Solen subfragilis* Eichwald, *Gastrana fragilis* (Linnaeus) and *Abra* (*Syndosmya*) *alba* (Wood).

Hence, the ecological requirements of the majority of the bivalve species, the abundance and ubiquity of *Obsoletiforma*, the genus that was fully adapted to life in extremely stressed environments that were unsuitable for other molluses, as well as the Na and Sr concentrations in the bivalve shells detected by Vasil'ev (2004) clearly illustrate that conditions in the Sarmatian Sea were other than normal marine [euhaline]. The lack of marine stenohaline elements suggests that the salinity was the main factor that controlled the species diversity.

All these features prove that, in the Early Sarmatian, the Paratethys was a huge mixo-mesohaline inland sea showing peculiar environmental features. Herein, the distribution and the species composition of the bivalve fauna are thought to have been controlled largely by salinity which, in the marginal parts of the Carpathian Foredeep Basin (as in the Vienna Basin), oscillated within the range 25–30% but in the Euxine-Caspian Basin System could drop down to 18% (Kojumdgieva 1969).



Text-fig. 12. Percentages of major bivalve groups collected from the Lower Sarmatian shallow sandy facies from the Pannonian Basin System and Euxine-Caspian Basin System after Paramonova (1994), and from: A – southern slopes of the Holy Cross Mts., Poland (after Krach 1967; Czapowski and Studencka 1990); B – western Ukraine (after Krach 1938, Kulchytsky and Kulchytsky 1983; Nevesskaja *et al.* 1993 and our studies); C – northwestern Bulgaria (after Kojumdgieva 1969); D – western Georgia (after Mushelishvili 1980) and E – northern Ustiurt and Turkmenistan (after Merklin and Nevesskaja 1955; Nevesskaja *et al.* 1993). Circle inside indicates total number of species of selected Paratethyan faunas. Map of the Paratethys after Paramonova (1994); Carpathian Foredeep Basin hachured

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APPENDIX

Compiled list of the bivalve species from the Late Badenian coralline algae-vermetid reefs (Roztocze and Medobory),based on papers of Teisseyre (1895, 1900) [Abbr. T]; Friedberg (1934–1936) [Abbr. F]; Korolyuk (1952) [Abbr. Ko]; Voloshina (1973) [Abbr. V]; Janakevitch (1977, 1993) [Abbr. Y]; Krach (1981) [Abbr. K]; Studencka (1994) [Abbr. S] and Chwiluk (2007) [Abbr. C]

Families and species	Localities	Poland			Ukraine	Moldova
1 annies and species		Węglin	Węglinek	Łychów	'n	Me
PALAEOTAXODONTA						
Nuculidae						
Nucula (Nucula) nucleus Linnaeus		S, C	K, S	K		
PTERIOMORPHIA						
Arcidae						
Arca (Arca) noae Linnaeus Acar clathrata (Defrance) Barbatia (Barbatia) barbata (Linnaeus) Barbatia (Barbatia) modioloides (Cantraine)		S, C S S, C	K, S K, S K, S	K, S K, S K, S	T T, X T, Ko, X T	V, Y Y
Anadara (Anadara) diluvii (Lamarck) Anadara (Anadara) anomala (Eichwald) Bathyarca pectunculoides (Scacchi)		S, C	K, S	K K	T	
Neotiidae						
Striarca lactea (Linnaeus) Arcopsis papillifera (Hörnes)		S, C C	K, S K	K K, S	T, X	
Limopsidae						
Limopsis (Pectunculina) anomala (Eichwald)		С	K, S			
Glycymeridae						
Glycymeris (Glycymeris) deshayesi (Mayer)		S	K, S	K, S	X	V, Y
Mytilidae						
Septifer oblitus Michelotti Brachidontes biali (Cossmann and Peyrot) Brachidontes marginatus (Eichwald) Mytilaster volhynicus (Eichwald) Gregariella coralliophaga (Chemnitz) Gregariella fuchsi (Sinzov) Musculus biformis (Reuss)		S, C S S	K, S K, S K S	K, S K	X T T	Y V
Musculus discors (Linneaus) Lithophaga (Lithophaga) lithophaga (Linnaeus) Lithophaga (Lithophaga) antillorum (d'Orbigny) Lithophaga (Lithophaga) bella Janakevich Lithophaga (Lithophaga) nigra (d'Orbigny)		S	K, S	K	T T, Ko, X X T, F	V, Y Y
Lithophaga (Leiosolenus) laevigata (Quay and Gaimarc Modiolus adriaticus (Lamarck) Dacrydium (Dacrydium) vitreum (Holböll) Botula subcordata (d'Orbigny) Modiolula phaseolina (Philippi)	l)	S	S K, S	S K	T	Y Y Y
Isognomidae						
Isognomon radiatus Hörnes			K	S		

Families and species	Localities	s Poland			Ukraine	Moldova
r annies and species		Węglin	Węglinek	Łychów	ń	Me
Pectinidae						
Pecten subarcuatus styriacus Hilber		S				
Gigantopecten nodosiformis (de Serres)						V
Oppenheimopecten aduncus (Eichwald)				K		V, Y
Oppenheimopecten revolutus (Michelotti)		S				
Hinnites crispus (Brocchi)					X	Y
Manupecten fasciculatus (Millet)					T, F, X	V, Y
Mimachlamys varia (Linnaeus)					T, F, X	V, Y
Crassodoma multistriata (Poli)		S, C	K, S	K, S	T, F, Ko, X	V, Y
Aequipecten scabrellus (Lamarck)					Т	
Aequipecten bryozodermis (Almera and Bofil)					Ť	
Aequipecten elegans (Andrzejowski)		S	K, S	K	Ko	V, Y
Aequipecten diaphanus (du Bois)			,		T	V, Y
Aequipecten malvinae (du Bois)					X	, -
Flexopecten lilli (Pusch)						V, Y
Flexopecten posthumus (Hilber)			K			., -
Flexopecten scissus (Favre)			K		T, X	V
Plicatulidae		<u> </u>			-,	•
Plicatula (Plicatula) mytilina Philippi		S	S			
Plicatula (Plicatula) gurgitis Pictet and Roux						Y
Plicatula (Plicatula) striata Defrance		S, C	K, S	K		Ÿ
Spondylidae		,	, , , , ,			
Spondylus (Spondylus) crassicosta Lamarck					T, X	Y
Spondylus (Spondylus) gaederopus Linnaeus		S	K, S	K, S	T, Ko, X	Y
Anomidae				,		
Pododesmus (Monia) squamulus (Gmelin)			S			
Anomia ephippium rugulosostriata (Bronn)		С	K, S	K	T	
Limidae						
Lima (Lima) lima (Linnaeus)		S, C	K, S	K, S	T, F, Ko, X	V, Y
Limatula subauriculata (Montagu)		I	K	S		,
Gryphaeidae		•				
Neopycnodonte navicularis (Brocchi)		S, C	K, S, C	K, S	T, X	Y
Ostreidae						
Crassostrea gryphoides (Schlotheim)		С			Ko	
Ostrea digitalina (Eichwald)			K	K	T, Ko, X	V, Y
HETERODONTA					•	•
Lucinidae						
Codakia (Codakia) leonina (Basterot)		1				V
Ctena (Ctena) decussata (da Costa)		S, C	K. S	K. S	T. X	V
Linga (Linga) columbella (Lamarck)] 5, 0	K, S K	K, S K	X	•
Loripes (Loripes) dujardini Deshayes			K	K	Λ	
Loripes (Microloripes) dentatus (Defrance)		S, C	S	K		
Megazinus (Megazinus) incrassatus (du Bois)] 5, 0		IX	X	Y
			l v c	I C	X X	I
Megazinus (Megazinus) transversus (Bronn)		C	K, S	K, S		Y
Lucinoma borealis (Linnaeus)			K, S	K	T, Ko, X	Y
Lucinella divaricata (Linnaeus)				S		

Localitie Families and species	es	Poland			Moldova
1 annuts and species	Węglin	Węglinek	Łychów	Ukraine	M
Thyasiridae					
Thyasira (Thyasira) flexuosa (Montagu)			S		
Ungulinidae	-		-		•
Diplodonta (Diplodonta) rotundata (Montagu)		S	K		
Chamidae					
Pseudochama (Pseudochama) gryphina Lamarck		K		T	
Chama (Psilopus) gryphoides Linnaeus	S, C	K, S	K, S	T, F, X	V, Y
Chama (Psilopus) minima Toula				T	Y
Erycinidae					
Lasaea rubra (Montagu)	S				
Kelliidae					
Kellia suborbicularis (Montagu)				X	
Bornia (Bornia) sebetia (da Costa)	S	K			
Mioerycina coarctata (Wood)		S			
Montacutidae	•		•		•
Montacuta substriata (Montagu)		K			
Carditidae	•		•		•
Cardita calyculata (Linnaeus)		K		X	
Cardita elongata (Bronn)		K			Y
Carditamera (Carditamera) auingeri (Hörnes)		K			
Glans (Centrocardita) rudista (Lamarck)	S, C	K, S	K		
Cardites partschi (Münster)	S	K, S	S		V
Astartidae	•				•
Astarte (Astarte) waeli Glibert			S		
Cardiidae	•				•
Acanthocardia (Acanthocardia) brocchii (Mayer)					V
Parvicardium holubicense (Hilber)	S	K	K		
Parvicardium papillosum (Poli)		S			
Parvicardium sonense (Cossmann)	S, C				
Parvicardium subhispidum (Hilber)	C	K	K		
Plagiocardium hirsutum (Bronn)		K, S	K		
Obsoletiforma vindobonensis (Laskarew)		S			
Discors spondyloides (Hauer)		S		X	
Mactridae		-			
Lutraria (Lutraria) lutraria Linnaeus					Y
Lutraria (Psammophila) oblonga (Gmelin)				X	
Mesodesmatidae	-		<u> </u>		-
Ervilia pusilla Philippi	S	K, S	K		
Psammobiidae	-				
Gari (Gari) elatior (Cossmann and Peyrot)					Y
Kelliellidae		-			
Alveinus nitidus (Reuss)	S	K, S	K		
Trapeziidae					
Coralliophaga (Coralliophaga) lithophagella (Lamarck)	S	K, S	K	X	Y
Coralliophaga (Coralliophaga) transylvanica (Hörnes)	S			F	V, Y
1	~				. , .

Localities Families and species	Poland			Ukraine	Moldova
Tummes and species	Węglin	Węglinek	Łychów	Ď	Ж
Veneridae					
Venus (Venus) subrotunda Defrance	S	K, S	K		
Venus (Venus) tauroverrucosa (Sacco)	S	K, S	K, S	Ko, X	
Venus (Ventricoloidea) nux (Gmelin)	S	K	S		
Venus (Ventricoloidea) libella (Rayneval, Hecke and Ponzi)	S	S	K, S	T, Ko, X	V
Circomphalus subplicatus (d'Orbigny)		K	,		
Gouldia (Gouldia) minima (Montagu)	S, C	K, S	K, S		
Dosinia (Pectunculus) exoleta (Linnaeus)				X	Y
Irus (Irus) irus (Linnaeus)	S	S	K, S		
Timoclea (Timoclea) sobieskii (Hilber)	S, C	K, S	K	T	
Petricolidae					
Petricola (Lajonkairia) rupestris (Brocchi)				T, X	
Myidae					
Sphenia anatina (Basterot)	S			X	
Corbulidae					1
Corbula (Varicorbula) gibba (Olivi)	С	S	K	T	
Gastrochenidae					1
Gastrochaena (Gastrochaena) dubia (Pennant)				F, X	V, Y
Gastrochaena (G.) lata Dollfus and Dautzenberg	S	K			
Gastrochaena (Gastrochaena) intermedia Hörnes		S		T, F, X	Y
Hiatellidae	_				
Hiatella (Hiatella) arctica (Linnaeus)	S	K, S	K	T	
Pholadidae					
Pholas cf. bulgarica Toula				T	Y
Jouannetia (Jouannetia) semicaudata DesMoulins				F, Ko, X	Y