

Traces of drilling predation in the Upper Badenian (Middle Miocene) molluscs from the Rakovica stream (Belgrade)

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Abstract

The palaeoecology of fossil molluscs of Serbia is insufficiently studied. Drilling predation indicates interactive relationships among Middle Miocene Badenian molluscs from the Rakovica sands. These sands are present in the Rakovica stream valley (southern part of Belgrade), and well-known data about the fauna has existed since the end of the XIX century. The collected material (one bulk sample) from the section was used for studies that included 2301 shells of molluscs (1617 of gastropods and 684 of bivalves). Among them were specimens with predatory drill holes. Determining the value of drilling frequency (DF) and prey effectiveness (PE) facilitates identification of the relationship between shell-drilling predators and their prey. Based on analysis of the overall association, carnivorous gastropods were dominant in the sample, comprising more than fifty percent (52.32%) of all gastropod specimens. In addition, they constitute a large percentage of the total sample (43.19%). The largest number of victims was observed among bivalves, which are indicated by a DF of 16.96%. The results were compared with other localities of Miocene age in Paratethys and with studies on the Miocene sediments from the Boreal and the Atlantic Provinces. These comparisons show that PE and DF are very similar to results from the Central Paratethys, but that they are significantly higher than in the other areas mentioned.

Keywords: Gastropods, Bivalves, Statistical analysis, Predator-prey interactions, Palaeoecological relations

1. INTRODUCTION

Traces of biotic drillings found on skeletons of marine invertebrates provide arguably the richest source of quantifiable data on prey-predator interactions available in the fossil record (KOWALEWSKI, 2002). Indeed, many studies of biotic interactions in the geological past have focused on drilling predation (VERMEIJ, 1982, 1987; VERMEIJ & DUDLEY, 1982; BAUMILLER, 1996; HOFFMEISTER & KOWALEWSKI, 2001; SAWYER & ZUSCHIN, 2011; CHATTOPADHYAY & DUTTA, 2013). The overall patterns of drilling predation are well established on Cenozoic molluscs from the Atlantic coast of North America (KELLEY & HANSEN, 1993, 1996, 2006), but there has been considerably less works conducted in Europe. Relevant studies of drilling predation on molluscs from the Miocene of Central Paratethys (HOFFMEISTER & KOWALEWSKI, 2001; SAWYER & ZUSCHIN, 2011) did not include any data from Serbia, so details of predator-prey interactions in the marine Middle Miocene from this part of the southeastern margin of the Pannonian basin remained largely unknown.

The Rakovica stream („Rakovički Potok”) near Belgrade represents one of the richest Middle Miocene (Badenian) fossiliferous sites in Serbia and has been the subject of geological and palaeontological studies for more than a century. PAVLOVIĆ (1890, 1893, 1922, 1925) and PAVLOVIĆ & PETKOVIĆ (1903) studied the fossil fauna itself, while LUKOVIĆ (1922), STEVANOVIĆ & STEPANOVIĆ (1939), STEVANOVIĆ (1951) and EREMIJA (1977, 1987) focused mainly on the stratigraphy of the site in the regional comparative context. PAVLOVIĆ (1925) was the first to note traces of biotic drillings on fossil specimens from

the Rakovica stream. He discovered that drilled shells belonged to ten gastropod and four bivalve species, and he assumed that these biotic boreholes were produced by predatory snails (*Natica* and *Conus*) found among other taxa on the site. Later study by KOHN (1983) reported that drilling predation is characteristic for *Naticidae* and *Muricidae*. Similar palaeoecological observations were discovered by STEVANOVIĆ (1970), who described traces of predation on Badenian shells collected in the vicinity of Belgrade, and more recently by JOVANOVIĆ (2002), who examined a Badenian fauna from Golubac, north-eastern Serbia. However, none of these studies focused on drilling predation and they were not carried out in a systematic manner. In order to fill this gap in knowledge, we present here the first detailed report of predatory behaviour within molluscs from the Middle Miocene of Serbia, which includes the comparison with the available data for Paratethys, and the Boreal and North Atlantic Provinces (HOFFMEISTER & KOWALEWSKI, 2001, KELLEY & HANSEN, 2006, SAWYER & ZUSCHIN, 2011).

2. GEOLOGIC SETTING

The fossil sample used for the study was collected from the Rakovica stream section, („Rakovički Potok”) located on the left bank of Rakovica creek in the southern part of Belgrade (WGS 84, 44°43'58", 20°30'27"). In Serbia, the site represents a classic locality of the sandy facies of the Badenian (Middle Miocene), the so-called Rakovica sands which are rich in marine fossils. It is located on the Basic geological map at scale 1:100000, sheet Pančevo (IVKOVIĆ, 1966). This area, based on main stratigraphic and tectonic studies, is a composite geological setting represented by block (horst and graben) structures. In this relatively

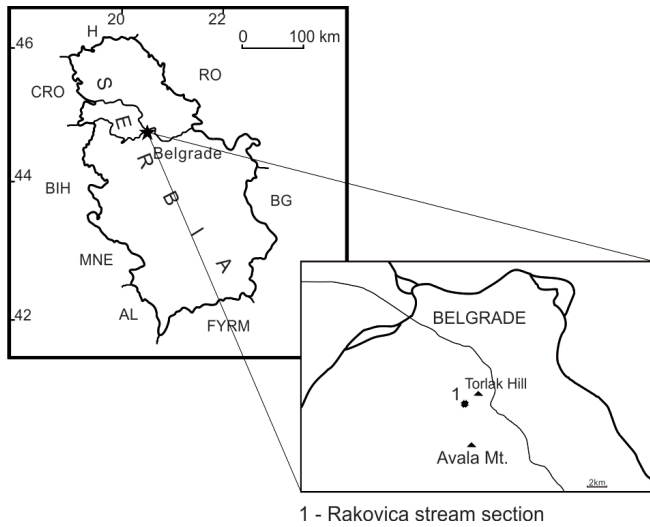


Figure 1. A simplified geographic position and location of the studied area.

small area and during the younger phases of Nealpine tectonics there were significant different movements which formed a modern relief. The Torlak hill is a horst structure with Mesozoic rocks in its core part, while the slopes are composed of different Badenian and Sarmatian deposits (MAROVIĆ et al., 2007). Further downstream from the Avala road, in the middle part of Rakovica stream, there is a small graben structure which is part of the Beli Potok graben, which is filled with the upper Miocene sediments (Pannonian and Pontian) as well as those of middle Miocene (Sarmatian) age. The Torlak horst and the Beli Potok graben are separated by the so-called Rakovica fault. These geological structures are characterized by large differential movements along the fault with a vertical displacement of more than 200 m. For example, in borehole KGK-14 below the Pontian sediments, at an altitude of 100 m, the Pannonian marls were discovered (KNEŽEVIĆ, 1989). However, just a few hundred metres away to north-east, in the Torlak foothill, the same Pannonian marls occur on the surface near 210 m. Similarly, at the top of Torlak hill, Badenian sediments are present at the surface at 336 m. All tec-

tonic movements took place during the late Miocene and Pliocene as well as the early Pleistocene. Based on strong vertical displacement along the block structures (uplift/subsidence) a composite hilly relief of this area was created.

The Rakovica sands are composed of a single uniform deposit, with a maximum thickness of 3 m at the studied exposure (Fig. 1). The section has no visible layers. It is dominated by gray-yellow quartz sands with unevenly distributed fossils, and poorly-cemented sands with hard sandstone lenses. The faunal assemblage of this locality is rich, both in terms of numbers and diversity of taxa, consisting of gastropods, bivalves, foraminifers, corals, bryozoans, ostracods, annelids, crabs (fragments of pincers), scaphopods, sea urchins (spine fragments), fish otoliths and shark teeth. Biostratigraphically, based on foraminifers, the sands from the Rakovica stream belong to the *Elphidium crispum*–*Ammonia viennensis* Ecozone, the upper Badenian Stage (PETROVIĆ, 1985; PETROVIĆ & ŠUMAR, 1990). The main taxa among forams includes: *Elphidium crispum*, *El. fichtelianum*, *Ammonia viennensis*, *Borelis melo*, *Spirolina austriaca*, *Asterigerinata planorbis*, *Cibicidoides cf. lobatulus*, *Lenticulina sp.*, *Quinqueloculina sp.*, *Planostegina sp.* Moreover, numerous ostracods including *Aurila punctata*, *A. cicatricosa*, *Cletocythereis haidingeri*, *Falunia plicatula*, *Cnestocythere truncata*, *Costa edwardsi*, *Tenedocythere sulcatopunctata*, *Pokornyella deformis*, *Bairdopipilata subdeltoidea*, *Loxoconcha hastata*, *Callistocythere canalicullata*, etc. were found. A similar exposure is located in the Belgrade City centre, beneath the Belgrade Fortress, where the sands lie next to the Miocene marine reef „Kalemegdan” (a geoheritage site), mostly composed of coralline alga *Lithothamnium* (EREMIJA, 1977). Although it forms a part of the same geological unit (the Rakovica sands), the faunal assemblage from the Belgrade Fortress is not nearly as rich as in the Rakovica stream. Nevertheless, it would be interesting to sample this exposure too, but since it is located in the zone of the protected geoheritage site, this was impossible.

Since the exposure is relatively small and lithologically uniform, and because it will probably become a geoheritage site soon, we did not want to damage the site by taking multiple sam-

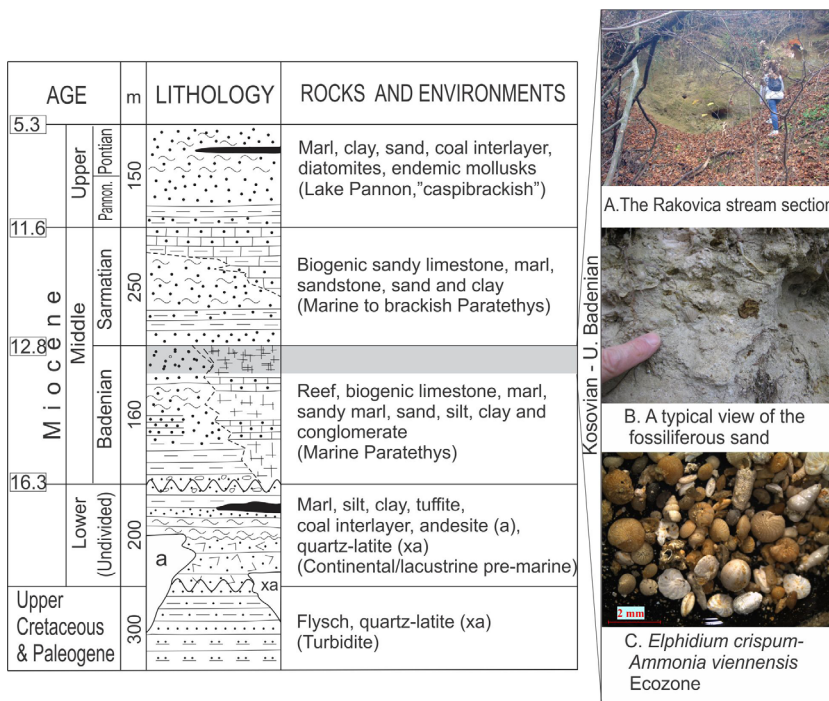


Figure 2. A general stratigraphic column of the Miocene of Belgrade area (modified after SCHWARZHANS et al., 2015). A gray rectangle marks the stratigraphic position of the studied sediments. Age of the Badenian regional stage based on HOHENEGGER et al., 2014.

Table 1. The list of species recovered from Rakovica sample, with numbers of specimens/valves (n) in parantheses.

Class	Species (n)	
Gastropoda	Acirsa drevermani (18), Acteocina lajonkaireana (15), Alaba costella anomala (127), Alvania oceani (31), Alvania productilis (1), Ancilla glandiphormis (25), Athleta ficulina (67), Athleta pirulaeformis (5), Athleta rarispina (10), Bittium spina (95), Buccinum limatum (11), Calyptrea chinensis (7), Cerithiopsis bilineata (1), Cerithiopsis opaca (15), Cerithium crenatum (17), Cerithium procrenatum (6), Clavata capgrandi (10), Clavata asperulata (29), Conus dujardini (21), Conus fuscocingulatus (96), Conus granularis (2), Euthria intermedia (5), Fusinus subrugosa (6), Fusinus valenciensis (1), Hydrobia hoernesii (116), Mangelia perpulchra (25), Marginella cratoformis (27), Marginella haueri (7), Marginella minuta (10), Mitrella bitneri (32), Mitrella fillisae (6), Mitrella hilberii (53), Murex granularis (3), Nassa badensis (81), Nassarius seraticosta (78), Natica millepunctata (22), Natica redempta (27), Neritina picta (21), Odontostoma plicatum (10), Oxistella patula orientalis (96), Pyramidella plicosa (12), Retusa truncatula (69), Ringicula buciniae (6), Rissoa turricula (42), Rissoina pusilla (8), Sandbergeria perpusilla (125), Scala tenuicosta (2), Scaphander lignaris (1), Strioterebrum basteroti (7), Terebra fuscata (2), Turricula miocenica (13), Turris disjuncta (18), Turritella badensis (6), Turritella bicarinata (2), Turritella subangulata (41), Turritella subangulata pulchra (8)	
	Bivalvia	Glycymeris glycymeris (91), Cardites partschi (35), Euripicardium multicostatum (22), Clausinella basteroti (22), Loripes dentatus (158), Anadara diluvii (62), Nucula (Nucula) nucleus (17), Gouldia minima (168), Tellina donacina (41), Linga (Linga) collumbela (14), Corbula carinata (24), Parvicardium papillosum (2), Cubitostrea digitalina (9), Glycymeris obtusata (19)

ples. Therefore, after we conducted a detailed examination of the entire exposure, we decided to collect only a single sample from the small surface of the vertical profile, located between 0.5 and 1 m from the accessible foothill (Fig. 2).

3. MATERIALS AND METHODS

The sample (bulk sediment) of about 10 kg was brought back to the laboratory for study. The sediment was processed using fine-mesh screens (0.15 to 0.80 mm) with seven sieves. Bivalves and gastropods were retained on screens 0.8; 0.7; and 0.6 mm. Traces of drilling have been identified on shells larger than 0.7 mm. All mollusc specimens were counted and examined for evidence of drilling predation under a binocular magnifier (REICHERT), with 20 x magnification for small and 2 x for large specimens. Initially, we counted the abundance at the different taxonomic levels (species, family, class and total). The frequencies of predator-prey interactions in the sample were analysed by calculating *drilling frequency* (DF), measuring the rate of prey mortality due to drilling predation, by dividing the number of specimens that contain at least one successful predation trace (DS) by the total number of specimens in the sample (n). For bivalves, the total number of specimens had to be corrected by dividing it by 2, in order to understand disarticulation of the shells after death. DF was calculated at family level (*Lower Taxon Frequency* according to KOWALEWSKI, 2002), but also at class and total assemblage levels (*Assemblage Frequency* according to KOWALEWSKI, 2002). Escalation parameters, (estimates that provide some measure of the predator's failure, or rather a prey's ability to resist predators), were assessed by calculating a relative frequency of failed predator attacks. This frequency is often referred to as *prey effectiveness* (PE), and is calculated by dividing the number of traces of unsuccessful attacks (ID) (incomplete, repaired and healed drill holes) by the total number of drilling attempts (ID plus number of complete drill holes, D) (KOWALEWSKI, 2002; SAWYER & ZUSCHIN, 2011). Chi-squared tests were used to compare drilling frequencies (on total-assemblage, class and family levels) and prey effectiveness (on total-assemblage and class levels) from the Rakovica sample with those published for Paratethys and other Miocene basins (HOFFMEISTER & KOWALEWSKI, 2001; KELLEY & HANSEN, 2006; SAWYER & ZUSCHIN, 2011). At family level, only data for the Central Paratethys (SAWYER & ZUSCHIN, 2011) were available. A 5% significance criterion ($\alpha = 0.05$) was applied to our statistical analysis, and an online interactive calculation tool was used for the chi-square tests (PREACHER, 2001).

4. RESULTS

A total of 2301 mollusc shells, consisting of 1617 gastropods and 684 bivalves, were recovered from the sample. 56 gastropod and

14 bivalve species (Tables 1 and 2) were identified. Evidently, gastropods dominated the sample both in terms of species richness and biomass. However, bivalves were more frequently at-

Table 2. Taxonomic summary of drill hole data from molluscs from the Rakovica site for the overall assemblage, classes and families. n = abundance (corrected to account for disarticulated bivalves), DS = number of shells with complete drill holes, D = number of complete drill holes, ID = number of incomplete drill holes, DF = drilling frequency, PE = prey effectiveness.

	n	DS	D	ID	DF (%)	PE (%)	
Total assemblage	1959	214	226	19	10.92	7.76	
Class <i>Gastropoda</i>	1617	156	168	13	9.65	7.18	
Class <i>Bivalvia</i>	342	58	58	6	16.96	9.38	
Gastropod families	<i>Epitoniidae</i>	18	1	1	0	5.55	0
	<i>Cylichnidae</i>	16	3	3	0	18.75	0
	<i>Litiopidae</i>	127	13	13	0	10.24	0
	<i>Rissoidae</i>	84	11	11	2	13.09	15.38
	<i>Olividae</i>	25	5	5	0	20	0
	<i>Volutidae</i>	82	0	0	0	0	-
	<i>Cerithiidae</i>	118	17	17	2	14.41	10.53
	<i>Buccinidae</i>	16	2	2	0	12.5	0
	<i>Calyptraeidea</i>	7	2	2	1	28.57	33.33
	<i>Cerithiopsidae</i>	16	3	3	0	18.75	0
	<i>Turridae</i>	82	6	7	0	7.32	0
	<i>Conidae</i>	119	4	6	0	3.36	0
	<i>Fasciolaridae</i>	7	1	1	0	14.28	0
	<i>Hydrobiidae</i>	116	7	7	0	6.03	0
	<i>Columbellidae</i>	38	4	4	0	10.53	0
	<i>Mitridae</i>	53	7	7	0	13.21	0
	<i>Muricidae</i>	3	0	0	0	0	-
	<i>Nassaridae</i>	159	8	8	0	5.03	0
	<i>Naticidae</i>	49	3	3	1	6.12	25
	<i>Neritidae</i>	21	0	0	0	0	-
	<i>Pyramidellidae</i>	22	5	5	2	22.73	28.57
<i>Trochidae</i>	96	2	2	1	2.08	33.33	
<i>Retusidae</i>	69	22	31	0	31.88	0	
<i>Ringiculidae</i>	6	0	0	0	0	-	
<i>Scaliolidae</i>	127	16	16	2	12.6	11.11	
<i>Terebridae</i>	9	0	0	0	0	-	
<i>Turritellidae</i>	75	13	13	1	17.33	7.14	
<i>Marginellidae</i>	44	1	1	1	2.27	50	
<i>Clavatulidae</i>	13	0	0	0	0	-	
Bivalve families	<i>Glycymerididae</i>	55	3	3	1	5.45	25
	<i>Carditidae</i>	17.5	4	4	0	22.86	0
	<i>Cardiidae</i>	12	1	1	0	8.33	0
	<i>Veneridae</i>	95	11	11	1	11.58	8.33
	<i>Lucinidae</i>	86	31	31	2	36.05	6.06
	<i>Arcidae</i>	31	5	5	0	16.13	0
	<i>Nuculidae</i>	8.5	2	2	0	23.53	0
	<i>Tellinidae</i>	20.5	0	0	2	0	100
	<i>Corbulidae</i>	12	0	0	0	0	-
	<i>Ostreidae</i>	4.5	1	1	0	22.22	0

tacked than gastropods, since drilling frequency was higher in the former (16.96%) than the latter (9.65%). In terms of prey effectiveness, bivalves (9.38%) were able to resist predator attacks more successfully than gastropods (7.18%).

The most abundant gastropod families (Table 2), with more than 115 specimens in the sample, were *Nassaridae* (159), *Litiopidae* (127), *Scaliolidae* (127), *Conidae* (119), *Cerithiidae* (118) and *Hydrobiidae* (116). With numbers between 96 and 44, the following families were also relatively numerous: *Trochidae* (96), *Rissoidae* (84), *Volutidae* (82), *Turridae* (82), *Turritellidae* (75), *Mitridae* (53), *Naticidae* (49) and *Marginellidae* (44). With abundances between 38 and 13, *Columbellidae* (38), *Olividae* (25), *Pyramidellidae* (22), *Neritidae* (21), *Epitoniidae* (18), *Cylichnidae* (16), *Buccinidae* (16), *Cerithiopsidae* (16), *Cylichnidae* (16) and *Clavatulidae* (13), were much less abundant. Six families were represented by less than 10 shells – *Terebridae* (9), *Calyptraeidea* (7), *Fasciolaridae* (7), *Ringiculidae* (6) and *Muricidae* (3). Six of 29 gastropod families were never drilled, but only two of those had abundances greater than 20 (*Volutidae* and *Neritidae*). Among the attacked families, the DF ranged from 2.08% (*Trochidae*) to 31.88% (*Retusidae*). Incomplete drill holes were observed in nine families, with PE ranging from 7.14% (*Turritellidae*) to 50% (*Marginellidae*); however, there were only one or two incomplete drillings per family. Most families were attacked between one and 19 times (successful plus unsuccessful attacks); the notable exception were *Retusidae*, with 31 complete, but no incomplete drill holes. Multiple drill holes were found in three families (*Turridae*, *Conidae*, *Retusidae*).

Three bivalve families dominated the sample (Table 2) – *Veneridae* (95), *Lucinidae* (86) and *Glycymerididae* (55). The *Arcidae* were represented by 31 specimens, *Tellinidae* with 20.5 and *Corbulidae* had 12; *Nuculidae* and *Ostreidae* had less than 10 specimens (8.5 and 4.5, respectively). The abundance data was corrected to account for disarticulated bivalves. Only one of 10 bivalve families was never drilled (*Corbulidae*), while one family showed traces of only two failed drilling attempts (*Tellinidae*).

Among those drilled, the DF ranged from 5.45% (*Glycymerididae*) to 36.05% (*Lucinidae*). Incomplete drill holes were present in four families, with the PE ranging from 6.06% (*Lucinidae*) to 100% (*Tellinidae*); however, as in gastropods, there were no more than two IDs per family. Most families were attacked (successful plus unsuccessful attacks) five times or less, except for the *Lucinidae* and *Veneridae*, with 33 and 13 attacks, respectively. No multiple drill holes were observed on bivalve shells.

Based on our analysis (Table 3) the total (mollusc) assemblage-level drilling frequency for the Rakovica sample (10.92%) is lower than the DF reported for the Paratethys province (15.2%) and significantly (two/three-fold) lower than those reported for the Boreal (22.4%), southeastern North Atlantic (23.5%) and US Atlantic coast (34.4%). However, the total assemblage-level DF for Rakovica is higher than the value reported for Central Paratethys (7.5%). These differences were all statistically significant, as showed by the chi-square tests. Comparisons of the assemblage-level DF for gastropods quite gave similar results and all differences were also statistically significant (Table 3). Alternatively, the assemblage-level DF values for bivalves, showed that only two comparisons were statistically significant. The DF for the Rakovica sample (16.96%) is almost two times higher than the DF reported for the Lower/Middle Miocene of the Central Paratethys (8.6%). Conversely, the DF for bivalves is two-fold lower than the DF reported for the US Atlantic coast (34.1%). Examination of the drilling frequencies for the Rakovica and Central Paratethys samples at the family-level, statistically significant differences only existed for three taxa (Table 4). Among the gastropods, the *Cerithiidae* were drilled almost twice as frequently in the Rakovica sample than in Central Paratethys (DFs are 14.41% and 7.6%, respectively). Among bivalves, the *Veneridae* show similar differences (DF in Rakovica sample is 11.58%, compared to 7.6% in Central Paratethys). *Lucinidae* were drilled five times more frequently in the Rakovica sample than in the Central Paratethys province (DFs were 36.05% and 7.1%, respectively).

Table 3. Statistical comparisons of total and phylum assemblage-level drill frequencies using chi-squared test. χ^2 = chi-square. Bold p-values are statistically significant at $\alpha = 0.05$.

Level	Sample	Drilled	Undrilled	DF (%)	χ^2	p-value	Source
Total assemblage							
	Rakovica	214	1745	10.92	–	–	Present study
	Central Paratethys	2324	28636	7.5	30.24	< 0.00001	SAWYER & ZUSCHIN, 2011
	Boreal	386	1336	22.4	88.71	< 0.00001	HOFFMEISTER & KOWALEWSKI, 2001
	Paratethys	156	868	15.2	11.5	0.000696	HOFFMEISTER & KOWALEWSKI, 2001
	Southeastern North Atlantic	27	88	23.5	16.67	0.000045	HOFFMEISTER & KOWALEWSKI, 2001
	US Atlantic Coast	11483	21945	34.4	458.99	< 0.00001	KELLEY & HANSEN, 2006
Gastropoda							
	Rakovica	156	1461	9.65	–	–	Present study
	Central Paratethys	1596	20698	7.2	13.75	0.000209	SAWYER & ZUSCHIN, 2011
	Boreal	284	875	24.5	111.72	< 0.00001	HOFFMEISTER & KOWALEWSKI, 2001
	Paratethys	84	515	14	8.66	0.003242	HOFFMEISTER & KOWALEWSKI, 2001
	Southeastern North Atlantic	22	45	32.8	36.59	< 0.00001	HOFFMEISTER & KOWALEWSKI, 2001
	US Atlantic Coast	4048	7573	34.8	415.48	< 0.00001	KELLEY & HANSEN, 2006
Bivalvia							
	Rakovica	58	284	16.96	–	–	Present study
	Central Paratethys	726	7747	8.6	28.562	< 0.00001	SAWYER & ZUSCHIN, 2011
	Boreal	102	461	18.1	0.196	0.657969	HOFFMEISTER & KOWALEWSKI, 2001
	Paratethys	72	353	16.9	0	1	HOFFMEISTER & KOWALEWSKI, 2001
	Southeastern North Atlantic	5	43	10.4	1.33	0.248805	HOFFMEISTER & KOWALEWSKI, 2001
	US Atlantic Coast	7435	14372	34.1	44.167	< 0.00001	KELLEY & HANSEN, 2006

Table 4. Statistical comparisons of family-level drill frequencies using chi-squared test. Bold p-values are statistically significant at $\alpha = 0.05$. Comparative data for the Central Paratethys comes from SAWYER & ZUSCHIN (2011).

Family	Rakovica DF (%)	Central Paratethys DF (%)	χ^2	p-value
<i>Rissoiidae</i>	13.09	10.9	0.398	0.53
<i>Cerithiidae</i>	14.41	7.6	6.689	0.0097
<i>Turridae</i>	7.32	8.6	0.119	0.730122
<i>Nassaridae</i>	5.03	6.8	0.742	0.39
<i>Pyramidellidae</i>	22.73	9.4	2.377	0.12
<i>Naticidae</i>	6.12	12.9	1.88	0.17
<i>Veneridae</i>	11.58	6	4.065	0.043781
<i>Lucinidae</i>	36.05	7.1	58.459	< 0.00001
<i>Arcidae</i>	16.13	4.7	3.776	0.051993

Due to the small number of unsuccessful drilling attempts (ID) in our sample and the lack of the appropriate comparative data, prey effectiveness could only be studied and tested for statistical significance in a very limited manner (Table 5). On the total assemblage-level, molluscs from Rakovica were less able to resist predator attacks than those from the Boreal and Paratethys province in general. When compared to Central Paratethys, the frequency of failed predator attacks on gastropods alone showed only a slightly lower value (PEs for Central Paratethys and Rakovica were 7.4% and 7.18%, respectively). Compared to Central Paratethys (6.3%), bivalves from Rakovica showed a higher PE value (9.38%).

5. DISCUSSION

The study of predator-prey interactions by calculating and comparing drilling frequency and prey effectiveness data is a common and widely used approach in fossil and modern environments. Although the drilling data for lower taxa (species, genus, family) probably provide the most biologically meaningful analysis of predator-prey interaction in the fossil record (KOWALEWSKI, 2002), assemblage-level analysis is more useful in the pragmatic sense. This is because assemblage-level data can be computed for any fossil sample and thus can be used for analytical comparisons throughout the fossil record. However, assemblage-level analyses are quite problematic, since they often mix habitats, combine prey with different morphological and ecological characteristics and do not take into account other, fine-scale palaeoecological data. A detailed review of the advantages and disadvantages of this method is outwith the scope of this paper, but can be seen elsewhere (KOWALEWSKI, 2002; LEIGHTON, 2002; VERMEIJ, 2002).

In this paper, the assemblage-level, class-level and family-level drilling data was calculated for the Upper Badenian strata

at the Rakovica stream in Belgrade, and compared to available data for Miocene provinces (Central Paratethys, Paratethys in general, Boreal, Southeastern North Atlantic and United States Atlantic Coast). This study is the first of this kind to be conducted on a sample originating from the Southern part of the Central Paratethys province.

As some of the published studies have already shown (HANSEN & KELLEY, 1995; HOFFMEISTER & KOWALEWSKI, 2001; SAWYER & ZUSCHIN, 2011), predation trace data from a single horizon, locality or province can vary significantly, due to the problem of spatial variation. This problem can possibly be solved by calculating average values derived from multiple samples (HOFFMEISTER & KOWALEWSKI, 2001) and was used in this study. For the reasons briefly explained above, it was not possible to take multiple and spatially separated samples from the Rakovica sands, therefore our sample may misrepresent the locality. However, the sample is relatively large (almost 2000 specimens) and there is a good chance that the sampling error is not high.

Based on the studies of lithological composition, presence of the diverse marine fauna (e.g. molluscs, foraminifers, and ostracods), and local palaeogeographical setting, it can be concluded with reasonable certainty that the Rakovica sands represented a shallow marine (littoral) environment during Late Badenian time (MAROVIĆ et al., 2007). The waters in this part of Central Paratethys were warm, since they were positioned in the subtropical climatic zone (KOVAČ et al., 2007). The presence of the warm-loving benthic fish (family *Gobiidae*) at the Rakovica stream (NELSON, 2006) supports this view. In this shallow water environment, the salinity was normal, with an occasional brackish influence, confirmed by discovery of the mixed assemblage of typical marine (corals, sea urchins) and euryhaline fauna (*Cerithiidae*, *Hydrobiidae* and *Lucinidae*). Discovery of scarce fragments of corals and echinoderms also indicates more dynamic conditions, water fluctuations and higher energy of water than the salinity. Some ostracods (*Callistocythere*, *Aurila*, *Loxoconcha*) suggest the upper part of the infralittoral zone (up to 40m, ZORN, 2003). The Rakovica ostracod fauna lived in shallow (about 50 m deep), warm, and clear waters, connected to a deeper sea, occasionally exposed to freshwater inflows. The finding of the foraminifer genus *Borelis* indicates very warm water and implies tropical to subtropical water temperatures. A similar indication was given by SZCZECURA & ABD-ELSHAFY (1988) and RUNDIĆ (1992) from the Badenian deposits of North Africa and NE Bosnia and Herzegovina. Somewhere, a very steep coast could be responsible for the extreme mixing of the marine fauna and also explains some brackish/terrestrial faunal elements at the sampling locality.

Table 5. Statistical comparisons of total assemblage and phylum-level prey effectiveness using chi-squared test. Bold p-values are statistically significant at $\alpha = 0.05$.

Level	Sample	D	ID	PE (%)	χ^2	p-value	Source
Total assemblage							
	Rakovica	226	19	7.76	–	–	Present study
	Central Paratethys	2324	165	6.6	0.45	0.502335	SAWYER & ZUSCHIN, 2011
	Boreal	386	77	16.63	10.768	0.001033	HOFFMEISTER & KOWALEWSKI, 2001
	Paratethys	156	3	18.87	6.449	0.011101	HOFFMEISTER & KOWALEWSKI, 2001
Gastropoda							
	Rakovica	168	13	7.18	–	–	Present study
	Central Paratethys	1596	58	7.4	5.926	0.014919	SAWYER & ZUSCHIN, 2011
Bivalvia							
	Rakovica	58	16	9.38	–	–	Present study
	Central Paratethys	726	107	6.3	4.466	0.034576	SAWYER & ZUSCHIN, 2011

Most of the identified bivalve taxa lived as infauna, buried in soft substrate on the seabed. They were sustained by filtration of suspended food, such as plankton, algae and other water-borne nutrients and particles (*Cardiidae*, *Veneridae*, etc.), or by chemosynthetic bacteria (in the case of *Lucinidae*). Carnivorous gastropods dominated the sample, comprising more than fifty percent (52.32%) of all gastropod specimens, and also a large portion of the total sample (43.19%). The most numerous of these were *Nassaridae*, *Conidae*, *Turridae* and *Volutidae*. Two families of predators (*Naticidae* and *Muricidae*) that were most likely responsible for the drill holes were observed in our sample. These gastropods gain access to the soft parts of the prey by the radula.

Our results on drilling intensity showed that bivalves from the Rakovica sands were attacked almost twice as frequently as gastropods (Table 2). This is probably related to the specific mode of life of these molluscs (infauna) and their enemies, naticids. Alternatively, prey effectiveness data (Table 2) indicates that the bivalves were more successful at resisting predator attacks. Again, this may be because most bivalves from the sample lived as infauna, which is hard to reach for predators (BARNES et al., 1988). In contrast, most of the identified gastropod prey lived as epifauna; and this makes them less accessible to infaunal predatory naticids, which constitute the majority of drilling predators in our study.

Most of the mollusc shells showed only traces of a single (successful) drilling attempt. Multiple drill holes were found only in three gastropod families (*Turridae*, *Conidae* and *Retusidae*) and only on a single specimen from each group. Several scenarios could explain these cases of multiple drilling. We could imagine more than one predator attacking the prey at the same time, but it could also be the case that individual drillings were made at different times (KITSCHHELL, 1986), by the same or a different predator. Also, a predator could have been attacking an empty shell (HOFFMAN et al., 1974). Unfortunately, experimental studies (HUTCHINGS & HERBERT, 2013) failed to solve this problem.

Six gastropod families (*Volutidae*, *Muricidae*, *Neritidae*, *Ringiculidae*, *Terebridae*, *Clavatulidae*) and one bivalve family (*Corbulidae*) were never drilled; also, *Tellinidae* showed only failed drilling attempts. This is probably because many of these lived buried deep in the sediment similar to the representatives of families *Tellinidae*, *Corbulidae* and *Volutidae* and relatively thick shells (*Volutidae*). The most numerous family (82 specimens) with no drillings on their shells were the *Volutidae*; interestingly, one specimen that belonged to this family as reported by SAWYER & ZUSCHIN (2011) also had no drill holes (although this could be just a coincidence, considering the small sample).

Here, naticids and muricids were considerably less abundant, forming 2.65% percent of the total sample. With just three specimens, the muricids were particularly rare. However, in the Central Paratethys sample published by SAWYER & ZUSCHIN (2011), these two predator families together comprise only 1.6% of the total mollusc sample. A considerably higher percentage (4.2%) of these predators was observed by KELLEY & HANSEN (2006) in the U.S. Atlantic Coastal Plains. Of course, we should keep in mind that these comparative figures were made on the basis of multiple samples from localities with different palaeoecological and stratigraphic settings. Moreover, 49 naticid specimens were attacked; all of these drillings were probably made by the members of the same taxa, because naticids are known for cannibalism (CHATTOPADHYAY et al., 2014a). Traces of predation muricids (a specific shape of drill hole; CARRIKER, 1981) were only determined on four gastropod shells. For a more precise as-

essment, a more detailed analysis should be made (ZŁOTNIK, 2001, CHATTOPADHYAY et al., 2014a), but it seems highly unlikely that the lack of infaunal prey was the cause of cannibalism among the naticids.

Comparisons of total assemblage-level and class-level drilling frequencies (Table 3) showed that the value for the Rakovica stream was significantly lower than the data reported for the Boreal, Paratethys in general, Southeastern North Atlantic and US Atlantic Coast. However, the value reported for the Central Paratethys was lower than the value reported here. These differences could be due to the fact that samples come from different stratigraphic settings: the Rakovica sands is Upper Badenian, the Central Paratethys sample comes from the Karpatian – Badenian, Paratethys sample is from Burdigalian – Serravallian, and Boreal, Southeastern North Atlantic and US Atlantic Coast are from Middle – Late Miocene. Other abiotic factors could also be responsible – differences in depth, seabed composition, salinity, temperature etc. Alternatively, the Central Paratethys represented an epicontinental sea with specific evolution, which lasted for less time than the evolutions of other basins used in our comparative analysis (RÖGL, 1998); therefore, we can assume that fossil communities were also distinctive (HARZHAUSER et al., 2003). This also means that communities of the Central Paratethys (SAWYER & ZUSCHIN, 2011) and Rakovica stream (which represents its southeastern part of Central Paratethys) are more similar to each other than to other basins; indeed, differences in DF values seem to confirm this. Also, we think that the higher DF in this study, relative to the Central Paratethys, is in accordance with the littoral character of the locality, since there is a negative correlation between drilling frequency values and increasing depth (WALKER, 2001; TOMAŠOVYCH & ZUSCHIN, 2009). It is believed that drillings are more frequent in warm, tropical environments, where mollusc numbers and diversity are far greater than in cold waters (VERMEIJ & ROOPNARINE, 2001, CHATTOPADHYAY et al., 2014b). Since there is actually a higher DF in the relatively cold realms of the Atlantic and Boreal, temperature was not the main cause for the observed differences. In the case of the Central Paratethys (SAWYER & ZUSCHIN, 2011) the low abundance of drilling predators may be a very good reason for low DF. Primarily, we must keep in mind that we are comparing a single locality with the cumulative data for entire marine realms, which included many datasets, from different types of sediments that were formed in different abiotic environments. This fact alone could be responsible for the large proportion of the differences observed.

Family-level DF values in this study were compared with data from the Central Paratethys (Table 4) and showed that *Cerithiidae*, *Veneridae* and *Lucinidae* were drilled significantly more frequently in our sample; all of these taxa represent non-predatory (grazers, suspension feeders and chemosymbionts, respectively) and euryhaline taxa. Their relatively high abundances and high DFs (especially for *Veneridae* and *Lucinidae*) could mean that they were preferred by predators; these taxa would have been more available in shallow waters with lowered salinity along the southeastern rim, than in the Central Paratethys in general.

Despite the methodological circumstances mentioned earlier, our comparisons of escalation data (Table 5) showed that molluscs from the Rakovica sands were possibly less successful in resisting predator attacks than those from Boreal and Paratethys provinces. This could be caused by biotic factors (such as a relatively higher number of predators etc.) or abiotic factors (such as a relative depth, seafloor composition etc.). When class-level es-

calation data from all parts of the Central Paratethys were compared with the SE parts in Belgrade, almost identical figures for gastropods were observed, while apparently bivalves from this study were more successful in resisting predator attacks. This too could be explained by the number of biotic and abiotic factors, or simply by a sampling artefact.

6. CONCLUSION

The analysis of predator-prey interactions in the southeastern part of Central Paratethys during the Badenian was conducted on the sample from the Rakovica stream locality (the Rakovica sands) in Belgrade. The fossiliferous sands were deposited in the littoral zone of a warm sea. The salinity in this part of the basin was normal, with an occasional brackish influence, as indicated by the mixing of typical marine and euryhaline faunas. From the biostratigraphic point of view, the Rakovica sands belong to the *Elphidium crispum* – *Ammonia viennensis* Ecozone (Upper Badenian). Statistical analysis of the rich gastropod and bivalve communities showed that bivalves were more frequently attacked by drilling predators than gastropods. Bivalves were also more successful in resisting predator attacks, probably due to the biotic factors, such as the dominant infaunal mode of life. Predatory gastropods such as the *Naticidae* and *Muricidae* families were mostly responsible for the drill holes examined in our study, but muricids were particularly rare.

In this study, comparisons with other Miocene provinces showed that the details of predator-prey interactions, matched (with minor deviations) the Central Paratethys, which indicates relative uniform palaeoecological conditions in the basin. However, there are relatively small differences between our results and data from all the afore-mentioned parts of the Central Paratethys province. At the Rakovica sands, there are higher DF and PE values because we were dealing with a single sample (environment), with specific local conditions such as temperature, salinity, depth etc. In contrast, all the other data used for comparison were cumulative, based on samples from different environments – littoral versus sublittoral, and estuaries versus fully marine settings and different strata. Other provinces mentioned here, show different results, both in terms of drilling intensities and escalation data.

Finally, we concluded that there is no general pattern for the interpretation of the palaeoecological conditions which have been responsible for the formation of different populations of fossil organisms and their predator – prey relationships.

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