

Tracing prey-predatory interactions in the Early Sarmatian (Mid-Miocene) shelly community from Rollsdorf Formation, Waldhof, Austria based on bioerosional observations

*Fúrásnyomok eredet- és eloszlásvizsgálata kora szarmata mészvázás közösségen
(Rollsdorf Formation, Waldhof, Austria)*

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Abstract – The investigation focuses on the distribution of drill-holes between taxa, identifying the most common preys and on the location and shape of drillings examining the preferences of potential predators in site-selectivity. These make it possible to trace the potential predators. The examined shells from the Rollsdorf Formation (Waldhof, Austria) represent an Early Sarmatian endemic epifaunal gastropod community in the western periphery of the Central Paratethys after the Badenian/Sarmatian extinction. To trace the most common prey around 3000 randomly selected specimens of *Potamides gamlitzensis*, *Mobrensternia*, *Hydrobia frauenfeldi*, *Neritina picta* and *Acteocina lajonkai* were examined giving a good outlook on the reduced diversity and abundance in the community after the environmental conditions had changed. Based on analogies dominant gastropod predator could be the survived epibenthic Muricid. However, the shape (the observed drill-holes on the Sarmatian epibenthic gastropod community show variety from nearly perfect circle to ellipsoid) and the location of drill-holes is versatile contrary to the assumption that only a Muricid predator could cause these deformations. Other circumstances suppose the abundance of Polychaeta worms and *Acteocina* species as possible attackers. Results also show that site-selection is clearly observable. The most common chosen sector in prey shells is the fifth, which is between 0°-90° angle on the second whorl. Thus, these drill-holes cannot be unambiguously connected to the activity of worms.

Összefoglaló – A tanulmányban vizsgált kora szarmata endemikus epibentosz gastropoda közösség (Rollsdorf Formáció, Waldhof, Austria) tipikus képviselője a badeni-szarmata határán a Központi-Paratethysben a környezeti adottságok megváltozása miatt bekövetkező kihalási esemény okozta diverzitás-csökkenésnek. A vizsgálat során arra kerestük a választ, hogy a fúrásnyomok hogyan oszlanak el a közösség taxonjai között, így mely taxonok tekinthetők potenciális prédának, továbbá, hogy a potenciális ragadozó a támadás helyének kiválasztás során rendelkezett-e preferenciákkal. A fúrásnyomok alakja és elhelyezkedése alapján a potenciális ragadozó(k) kilétére is fény derülhet. E célok érdekében mintegy 3000 véletlenszerűen kiválasztott gastropoda (*Potamides gamlitzensis*, *Mobrensternia*, *Hydrobia frauenfeldi*, *Neritina picta* and *Acteocina lajonkai* stb.) vázon végeztük el a fúrásnyomok fenti minta (alak, elhelyezkedés, gyakoriság) alapján történő kiértékelését. Irodalmi analógiák alapján feltételezhető, hogy a támadó gyakran a kihalási hullámot túlélő egyetlen epibentosz muricid faj lehetett. A fúráslyukak alakja és elhelyezkedése azonban nem teljesen támasztja alá a feltételezést. Más körülmények és szakirodalmi analógiák arra utalnak, hogy nem zárható ki Polychaeta férgek és a prédaként alig előforduló *Acteocina* faj tevékenysége. Az eredmények bizonyítják, hogy a helykiválasztás nem véletlenszerű: a leggyakrabban választott támadási felület a második csavarulat 0-90 fokos irányánál volt található. E fúrásnyomok azonban valószínűleg ne tekinthetők férgek tevékenységének.

Keywords: Central Paratethys, Sarmatian, drill-holes, Muricid, Polychaeta, *Acteocina*, site-selectivity

Tárgyszavak: Központi-Paratethys, szarmata, fúrásnyomok, Muricidae, Polychaeta, *Acteocina*, helyválasztási stratégia

Introduction

Waldhof is in the Western Styrian Basin about 1 km west of Wetzelsdorf, close to Graz. The Styrian Basin (see *fig. 1*) evolved during the Neogene as a western subbasin of the Pannonian Basin System. It consists of several smaller subbasins: these are the Western Styrian Basin, the Mureck Basin, the Gnas Basin, and the Fürstenfeld Basin. The nearly 400 km² basin at the eastern margin of the Eastern Alps contains considerable mass of Neogene sediments. Sediments of the Mid-Miocene Sarmatian Sea are known from numerous surface outcrops in this section such as Rollsdorf, Gleisdorf, Waldhof, Klapping, Waltra (HARZHAUSER & PILLER 2004 a-b).

The Sarmatian (c. 12.8-11.6 Ma before present) is the 1.5 Ma period of the Central Paratethys Sea, as regional stage between the marine Badenian and a lacustrine Pannonian stages. This time interval coincides with the nearly entire disconnection of the Paratethys (Sarmatian) Sea from the open ocean. This was the reason for the drastic changes in water chemistry (mainly the increased alkalinity) of Sarmatian Sea, and furthermore, for the collapse of previous Badenian marine communities (PILLER & HARZHAUSER 2005,

PILLER et al. 2007), resulting a 90% extinction rate (HARZHAUSER & PILLER, 2007). Primarily, based on the absence of stenohaline taxa (HARZHAUSER 2002), for a long time the thesis, that the salinity of the Sarmatian Sea was reduced, dominated (PAPP 1956, BODA 1959). However, as already discussed by PILLER & HARZHAUSER (2005), instead of the brackish Sarmatian Sea conception it has become evident from palaeoecological microfacial and geochemical subjects that normal saline and in some places hypersaline water conditions dominated the entire Sarmatian.

The gastropod assemblage of the Lower Sarmatian Rollsdorf Formation of the Waldhof Beds in the Western Styrian Basin from some outcrops already recultivated (*fig. 2*) is well-known by the palaeontological studies of PAPP (1952, 1956). In this shelly community of Waldhof Beds the endemic genus *Mobrensternia* (Stoliczka) belonging to the gastropod family *Rissoidea* is frequent. Thus, due to the mass-occurrence of the *Mobrensternia* species, the Waldhof Beds can be correlated to the Early Sarmatian *Mobrensternia* ecostratigraphic Zone, which coincides with the maximum transgression of the Early Sarmatian Sea (KOWALKE & HARZHAUSER 2004).

PILLER & HARZHAUSER (2005) mentions marine diatoms in addition to *Mohrensternia* in the study area, which allows nearly polyhalin condition.

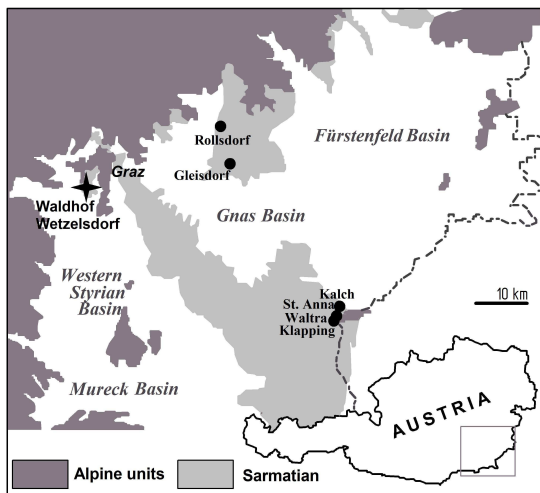


Fig. 1. Location map of the Styrian Basin and some locations of important Sarmatian outcrop redrawn from HARZHAUSER & PILLER (2004)

1. ábra. A Stájer-medence szarmata üledékei és ismert feltárásai HARZHAUSER & PILLER (2004) alapján

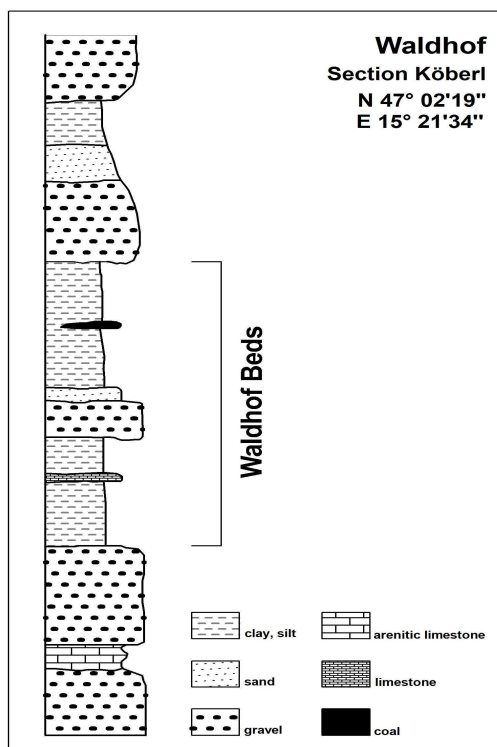


Fig. 2. Lithological profile about the former outcrop after RIEPLER (1988). The Waldhof Beds from the Rollsdorf Formation consist mostly of siliciclastic sediments. The clay, silt facies were sampled and the investigated specimens were collected from the site

2. ábra. A Waldhof-i feltárás litológiai profilja RIEPLER (1988) szerint. A döntően sziliciklasztos üledékekéből álló feltárás péletes fáciesű rétegeiből történt a mintavétel

Predatory drill-holes of gastropods are frequently revealed within the Sarmatian shelly fauna. Only two shell-drilling predatory taxa survived the Badenian-Sarmatian extinction event, the Muricid *Ocenebra striata* and the Naticid *Euspira helicina* (HARZHAUSER & KOWALKE 2002, HARZHAUSER & PILLER 2007, MANDIC et al. 2008).

The present study focuses on the identification of the possible attackers (site-selectivity, predator-prey relationships) based on drill-holes observed in the Early Sarmatian endemic mollusc fauna from the western margin of the Central Paratethys sea, Rollsdorf Formation, Waldhof.

Material

The number of investigated specimens is about 2900 belonging to the following taxa (table 1):

Neritina picta (formerly *Agapilia picta*, Ferussac, 1825): 161 specimens

Potamides gamlitzensis (formerly *Pirenella gamlitzensis*, Hilber, 1879): 99 specimens

Mohrensternia (Stoliczka, 1868): 489 specimens – such as *Mohrensternia hydroboides* (Hilber, 1897) *Mohrensternia sarmatica* (Friedberg, 1923) *Mohrensternia waldhofensis* (Kowalke & Harzhauser, 2004)

Hydrobia frauenfeldi (Hörnes, 1856): 1575 specimens

Acteocina lajonkareana (Basterot, 1825): 590 specimens

The majority of these epifaunal species was herbivorous, except for the carnivorous *Acteocina lajonkareana*.

	drill-holes	examined specimens	drilling % in taxon	drilling % in community	proportion of taxons (%)
<i>Neritina picta</i>	4	161	2.8	1	5.5
<i>Potamides gamlitzensis</i>	38	99	38.4	10	3.3
<i>Mohrensternia</i>	40	489	8.2	11	16.7
<i>Hydrobia frauenfeldi</i>	280	1575	17.8	78	54.0
<i>Acteocina lajonkareana</i>	1	590	0.2	0	20.0
Altogether	363	2914	12.4	100	100

Table 1. Distribution of drillholes among taxons and within the community

1. táblázat. A fúrások eloszlása a taxonokon és a közösségen belül, a taxonok részesedése a vizsgált anyagból

Methods

Drill-holes - regardless of their origin - were traced and revealed in each shell. Based on the geometric shape of these drill-holes the possible attacker(s) were identified.

Morphologies of predatory drill-holes in *Potamides gamlitzensis* were quantitatively described with flatness ratio (f) according to ISHIDA (2004):

$$f = \frac{d_{\min}}{d_{\max}}$$

Where d_{\min} equals the minimum diameter, d_{\max} is the maximum diameter of the internal hole. The hole is circular, if the value of the flatness ratio nears to 1.

For the purpose of further statistical investigations we examined the frequency (%) of drill-holes on each abundant taxons. Furthermore, each drill-hole was categorised as successful, unsuccessful or unfinished by the inner-outer diameter ratio. The drill-hole is considered successful, if the ratio is equal or greater than 0.5. In the case of unsuccessful predation the drill-hole inner-to-outer diameter ratio is less than 0.5, which is not large for the proboscis (KITCHELL et al 1986).

In the course of the quantitative analysis of site-selectiveness, all whorl on the shells was divided into four different sectors – with intervals ranging 0°-90°, 90°-180°, 180°-270° and 270°-360° degrees, where 0 is measured from the youngest part of the whorl, according to figure 3 –, modified after KOWALEWSKI (2002).

The number of drill-holes was evaluated in each sector. The surface of whorls is gradually reduced towards the axis, so it is probable, that more drill-holes occur on younger whorls, than on older ones. The area of whorls was measured on many specimens and instead of using the total number of drill-holes for each whorl or

sector, the number of drill-holes per unit area (drilling density) was used to calculate the distributions and to measure site-selectiveness. So the weighted number of drill-holes for each sector were calculated. Therefore a correctional factor was introduced calculated with the following formula:

$$a_i = \frac{A_i}{\sum A_i}$$

Where a_i is the relative surface and A_i equals with the surface of whorl. The drilling density (weighted number of drill-holes) is shown by this formula:

$$Dd_i = \frac{n_i}{a_i}$$

Where Dd_i (drilling density) equals the number of drill-hole n_i per the relative surface a_i . Tabulations were made for total complete drill-holes belonging to each sector with respect to the most frequent prey taxa.

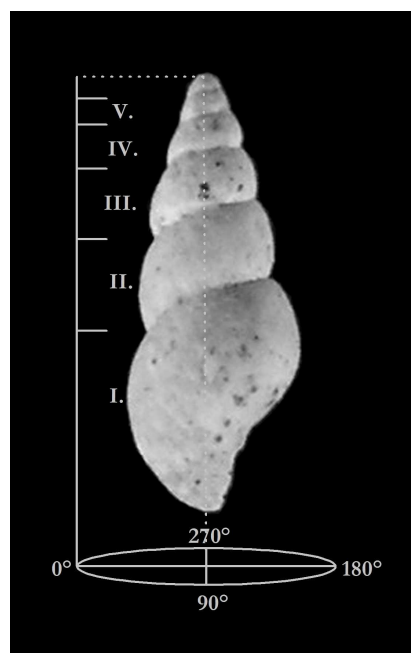


Fig 3. Scheme of shell divided into whorls and direction modified after KOWALEWSKI (2002)

3. ábra: a váz felosztásának vázlata irányok és kanyarulatok szerint, KOWALEWSKI (2002) után módosítva

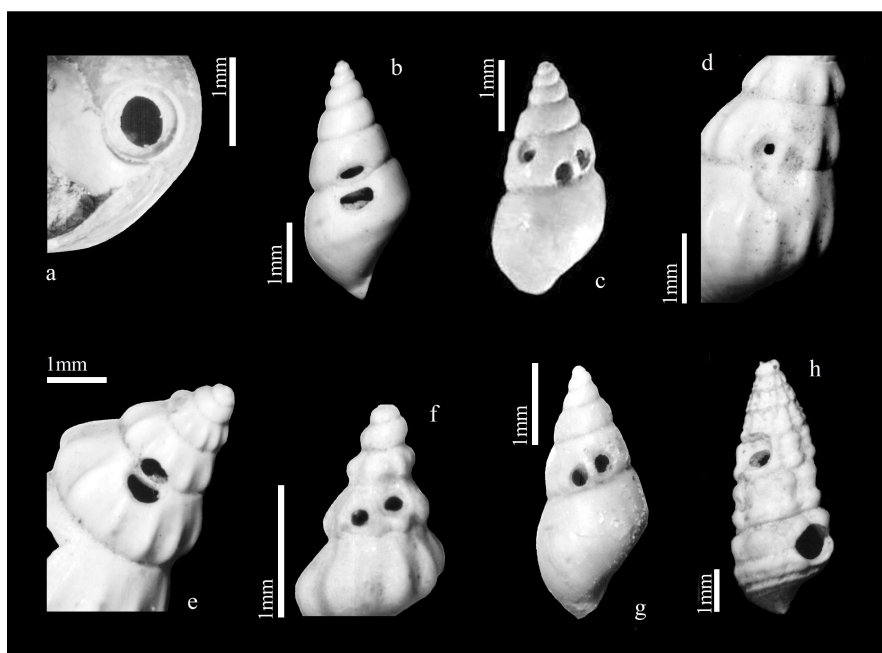


Fig. 4. Drill-holes in Early Sarmatian gastropods from Rollsdorf Formation, Waldhof. (a) complete (as successful) drill-hole in *Neritina picta* (Férussac, 1825). (b) Incomplete (unsuccessful) drill-hole in *Hydrobia frauenfeldi* (Hörnes, 1856) (c) multiple drill-hole in *Hydrobia frauenfeldi* (Hörnes, 1856) (d) Unfinished drill-hole in *Mobrensternia hydroboides* (Hilber 1897) (e) Incomplete (unsuccessful) drill-hole in *Mobrensternia hydroboides* (Hilber 1897). (f) multiple drill-hole in *Mobrensternia sarmatica* (Friedberg 1923). (g) multiple drill-hole in *Hydrobia frauenfeldi* (Hörnes, 1856). (h) multiple drill-hole in *Potamides gamlitzensis* (Hilber, 1879)

4. ábra. Fúrásnyom kora sarmata csigákon (Waldhof, Rollsdorf Formáció) (a) sikeres fúrás *Neritina picta* mészvázán (b) sikertelen fúrás *Hydrobia frauenfeldi* mészvázán (c) többszörös fúrásnyom *Hydrobia frauenfeldi* mészvázán (d) befejezetlen fúrás *Mobrensternia hydroboides* mészvázán (e) sikertelen fúrás *Mobrensternia hydroboides* mészvázán (f) többszörös fúrásnyom *Mobrensternia sarmatica* mészvázán (g) többszörös fúrás *Hydrobia frauenfeldi* mészvázán (h) többszörös fúrás *Potamides gamlitzensis* mészvázán

Regarding predator-prey interactions like site-selectiveness, the even distribution of drill-holes was challenged by KELLEY (1988) on bivalve. To examine the null hypothesis on gastropods, the distribution of boreholes was tested with One-Sample Kolmogorov-Smirnov test for normal, uniform, exponential and Poisson distributions using SPSS 15.0 for Windows. Histograms were also used to test the distributions and

show frequencies of drill-holes within whorls and within different directions. It is important to emphasize, that for the genus *Mohrensternia* no separate observations at the species level were made on drill-holes, since there is no notable difference between the *Mohrensternia* species regarding their morphology and height, that could have caused any significant change in the strategy of the predators.

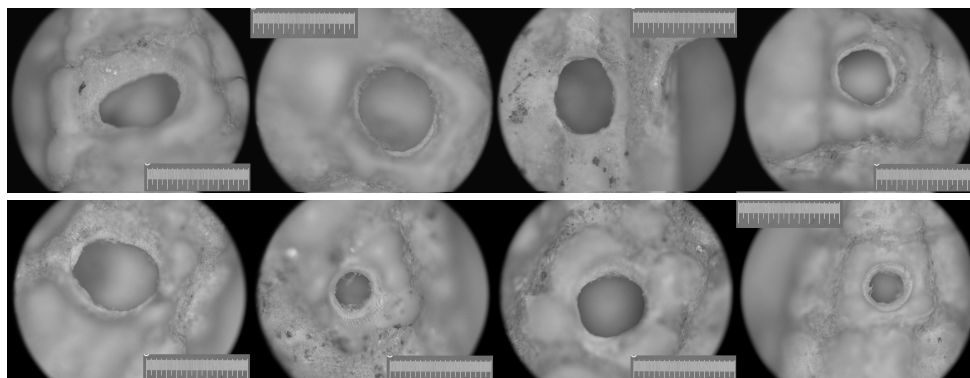


Fig. 5. Shape of drillholes in *Potamides gamlitzensis*. (HILBER, 1879) The scale is 1 mm. Pictures are taken from different parts of the shells, the resulting circular shape is the consequence of the field of vision in the microscope
5. ábra. Változatos formájú fúrásnyomok *Potamides gamlitzensis*. (HILBER, 1879) mérvázakon. A lépték 1 mm.

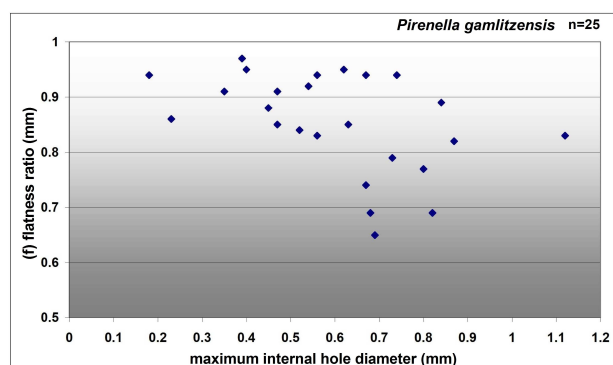


Fig 6. Deviation of drill-holes from the perfect circle in the shells of investigated *Potamides gamlitzensis* based on the (f) flatness ratio
6. ábra. A fúrásnyomok eltérése a tökéletes körtől a maximális átmérőhöz viszonyítva

Results

Numerous small, round or slightly oval holes can be observed on the shells from Waldhof. Drillings show different abundance on different gastropod taxa. Variability of the frequency (in percentage) ranges from 0.2 to 38.4 for the examined gastropod species (see fig 7). The frequency is the highest for *Potamides gamlitzensis* (38.4%), *Hydrobia frauenfeldi* (17.8%) and it is strongly underrepresented for the *Neritina picta* (2.4%) and *Acteocina lajonkai* (0.2%).

Some of the shells bear more than one drilling (fig. 4 c, f, g, h). The maximum value of the multiple drill-hole among the observed specimens is five, which were observed one juvenile *Hydrobia frauenfeldi*. However the ratio of multiple drillings among the species of the

community do not exceed 4-10% for the examined species, which means these were quite underrepresented.

The size of the drillings are different, which is in connection with the size of the prey shells. In the case of the greater (10-14 mm in height) and thicker *Potamides gamlitzensis* the internal diameter of the drillings is about 0.2-1.1 mm, while in the case of *Hydrobia* and *Mohrensternia* species with smaller (4-8 mm in height) and thinner shells this inner diameter is usually around 0.1-0.8 mm.

Based on the ratio of measurement of outer and inner diameter, the frequency of the successful drill-holes in percentage are high with regard to the three the most common preys. 67% of the observed holes were considered complete, 30 % incomplete, 2% unfinished in shells of *Potamides gamlitzensis*. In the case of *Hydrobia frauenfeldi* the results are: 66% complete, 25% incomplete and 9% unfinished. Concerning *Mohrensternia* 79% of the drill-holes were considered complete, 11% incomplete and 10% unfinished.

The shape of drillings is also different, which is demonstrated by the flatness ratio of ISHIDA (2004). The flatness ratio (f) of these holes in the shells of investigated *Potamides gamlitzensis* is between 0.69 and 0.97 showing variability from oval to circular shape (fig 5-6), although, the circular shape is more typical than oval. (mean f =0.86.).

The position of drill-holes (including all borings and complete separately) on shells of the three most common prey taxa (*Potamides gamlitzensis*, *Hydrobia frauenfeldi*, *Mohrensternia*) was examined for directions, whorls and sectors as well. Borings on the thick suture (see fig. 4 b, e) - occurred as well, their proportion reached 20-26%, for the different examined species. (These drillings were counted for both whorls in the statistics).

Significance levels in *table 2* represent the probability of abandoning the null hypothesis (test distribution is even), while it is true. For example, in the case of *Potamides gamlitzensis* the sig. 0.041 for uniform test distribution (tested for sectors) means, that the chance to commit a mistake when abandoning the null hypothesis (even distribution) is 4%, while the chance to commit mistake when abandoning normal distribution is 55%.

Although, it seems unlikely to maintain the relevance of the original null hypothesis (test distribution is even), nor the normal, neither the exponential, or Poisson distribution of the drill-holes can be proved, since either the significance values are not high enough for such a reliable statement, or there are two or more distributions with the same significance values (*Potamides gamlitzensis*, *Hydrobia frauenfeldi* according to whorls).

The small number of intervals (4 directions, 5 whorls) cannot produce or predict a reliable statement for these distributions investigated, however it is true that distributions are not uniform, rather unimodal or polymodal as histograms clearly indicate. In case of increasing the number of intervals (16-20 sectors), the difference between the significance values for the investigated test distributions is clearly observable, however still not high enough to predict normal distributions (not to mention the lack of continuous distribution) - as histograms indicate, rather polymodality can be observed (*table 3*).

In this study the hypothesis of even distribution of drill-holes on gastropods was examined and challenged, based on analogies investigated by KELLEY (1988) on bivalves. Observable preferences in site selectivity rendered the supposed even distribution a flawed hypothesis in our case as well.

Histograms clearly represent which drill-hole location was preferred as strategic location by the attacker. Distribution on histograms – indicating weighted number of drill-holes in different directions – is mostly polymodal with respect to the three most frequent prey taxa. Although, one may observe more than one overrepresented directions, it can be concluded that the direction between 0°-90° was among the most preferred.

Based on histograms, it is also observable, that in the case of *Mohrensternia* species and *Hydrobia frauenfeldi* the drill-holes are overrepresented in the second whorl, while in the case of *Potamides gamlitzensis* drill holes occur most frequently on the third whorl.

Histograms clearly indicate the preferences in site selection: the 5th sector is overrepresented for the three major taxa (second whorl, 0°-90°) sometimes accompanied by the 8th or 9th sector, causing polymodal distribution of drill-holes.

Identifying the potential predator - a discussion

It is not unambiguous to identify and assign drillholes to predatory organisms in case of dominantly small gastropod shells (*table 4*).

JEKELIUS (1944) observed similar drillings on Sarmatian gastropod shells in the Bánát analogous with our examinations. He claimed that these drillings on the juvenile *Cerithium* and small *Calliostoma*, *Acteocina*,

Hydrobia species originated from worms. However, modern descriptions regarding the drilling activity of Polychaeta (*Helicotaphrichnus*, BROMLEY, 1981) give detailed information about the position of drillholes. According to these descriptions the cylinder-shaped drillholes of Polychaeta can usually be found at the apertura of shells, and the line of the drilling follows the columella towards the apex (KERN et al. 1974, DÁVID 2005). If the drillholes on shells from Waldhof are made by Polychaeta, according to the description we should experience, that drillings mainly occur around the apertura of the shell. But after examining the distribution of drillholes, we concluded that around the apertura (sector 3 and 4) and the on whole 1st whorl, drillings are quite rare. Most of the drillings occur on the 2nd whorl considering the examined gastropod shells from Waldhof.

BODA (1959) in the clayey strata of the limestone quarry of Perpál (Hungary) found similarly small drillings (sometimes even 3-4 on one shell) on small-sized *Hydrobia*, *Mohrensternia* and juvenile *Cerithium* as we did in our examination. Few drillings were observed on *Neritina* as well, however these were rare, similar to the Waldhof material. These drillings were described as Muricid drillholes by Boda and some Muricid shells were also found among the community from Perpál (*Oichnus pimplex*, BROMLEY, 1981).

The Muricids were rather common carnivorous elements of the epifaunal mollusc assemblages in the Central Paratethys Sea in the Badenian, documented by at least 60 species. However, diversity of taxa was severely reduced during the Badenian/Sarmatian boundary. Altogether, one muricid species, the *Ocenebra striata* (Eichwald 1830) as survivor is investigated within the highly endemic Sarmatian marine fauna (HARZHAUSER & PILLER 2007, MANDIC et al 2008). The habitat of this gastropod family is the coastal marine environment, they avoid deep water and soft bottom (BROMLEY 1981, DAVID 1997). It is known that their preys are mainly epifaunal organisms (ARUA 1989). The process of their drilling is a combination of chemical and physical methods: acid dissolves the shell of prey and the radula makes a small drill hole with the mechanical abrasion. The shape of small holes by Muricid drilling gastropods are cylindrical with straight edges. In the case of successful drillings the external opening diameter of the drill-hole approximately corresponds with the internal opening diameter. Then the proboscis of the predator is able to penetrate fully into the shell of prey and feeding can take place efficiently. The activity of predatory gastropods considered unsuccessful, if the internal diameter of the boring is considerably smaller, than the width of external diameter. In this case the proboscis cannot get into the soft tissue trough this narrow opening. (HOFFMAN et al. 1974, BROMLEY 1981, HARPER 2006, WALKER 2007).

However we did not find Muricid *Ocenebra striata* shells, earlier PAPP (1952, 1956) described a Muricid species from the examined site, which proves their presence in the Waldhof community.

The examined gastropod shells belong to epibenthic communities such as the Muricids did, but the variability of drillholes (shown by the faltness ratio of ISHIDA 2004) may contradict to the statement, that Muricids committed the

drillings. This variability in the shape of drillings is noteworthy, since only one Muricid is known from the Sarmatian. The high percentage of drillings on the sutura may be confusing as well, since it would have meant a

failed strategy, as drillholes divided by the sutura are not wide enough for the proboscis. However this phenomenon is not unique for Muricid predators as GÖRÖG & SOMODY (1988) observed on Badenian gastropod shells.

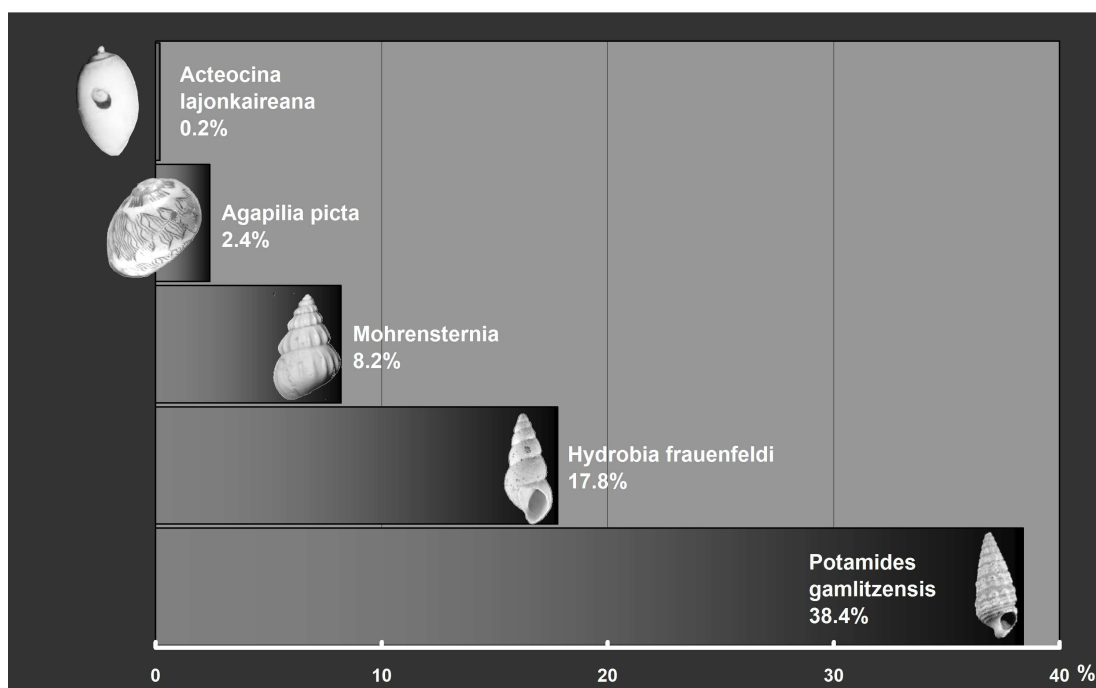


Fig. 7. Percentage frequency of drill-holes regarding the five prey taxa
7. ábra. Fúrásnyom gyakoriság (%)öt vizsgált taxonon

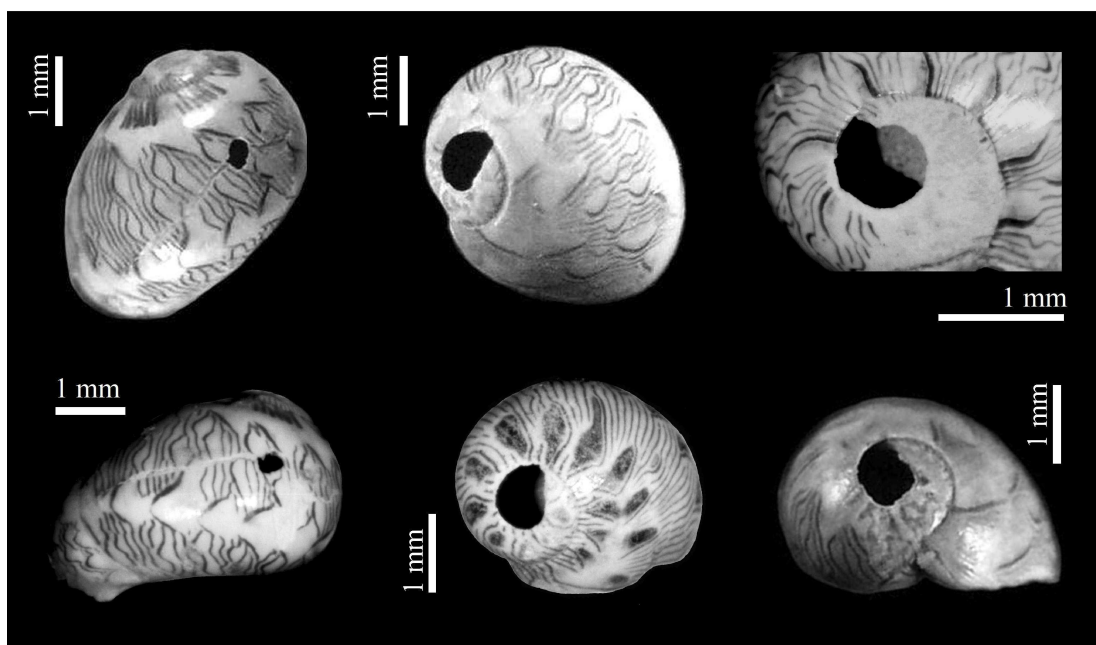


Fig. 8. Trace of damage on *Neritina picta* (FERUSSAC, 1825) from Rollsdorf Formation, Waldhof
8. ábra. Sérülésnyomok *Neritina picta* (FERUSSAC, 1825) mészvázakon (Waldhof, Rollsdorf Formáció)

It is also worth mentioning another species of the examined community, the *Acteocina lajonkareana*, which is a predator gastropod of small size. On 590 specimens only

one drilling was observed, which means that *Acteocina lajonkareana* may not be considered prey taxon. We may not exclude the possibility, that *Acteocina lajonkareana* can

also be responsible for the drillings on the examined small prey gastropods (as *Mohrensternia* and *Hydrobia*) in Waldhof, nevertheless the evidence of this poor, since this species probably used to feed on foraminiferae (MANDIC et al. 2008), as BAZAS & CARLE (1979) and SHONMAN & NYBAKKEN (1978) observed based on recent analogies. However foraminiferae suffered a greater extinction at the Badenian/Sarmatian boundary (60% at species level) (HARZHAUSER et al 2007), and their size reduced as well (even to >250µm) (SCHÜTZ et al., 2007), while *Acteocina lajonkairieana* survived, though became smaller.

Several remarkable characteristic damages, which are not clearly caused by shell boring gastropods, may be recorded on some *Neritina picta* shells (see fig. 8). The shape of these punctures (diameters 0.2-0.8 mm) is from nearly circular to irregular with sharp edge, which, in the majority of cases follows the outline of sutura. These damages may be similar to spearing stomatopod producing punctures (0.2-1.5 mm diameter), which is described by PETHER (1995) such as *Belichnus*, as new ichnogenus from Holocene. However, this similarity is not considered as identity, since the description of *Belichnus* concerned primarily the Holocene Tellinid bivalves in the Benguela region, Southwestern Africa.

Gonodactyloids are one of the major group of stomatopods, that attack their preys by shell-smashing or shell-spearing predatory processes (ZUSCHIN et al 2003). Damages, caused by Stomatopod crustaceans, as trace are infrequently documented from Neogene fossil record WALKER & BRETT 2002). Predatory damages of *Gonodactyloid* (a smashing stomatopod) on some gastropods are known from Miocene Central Paratethys (BALUK, & RADWANSKI, 1996). Additionally, stomatopod shell damage on several gastropods from Early Miocene (Egerian), Hungary are mentioned by DAVID (2005). However, diameters of small holes on the investigated *Neritina picta* specimens are commonly smaller than diameters of punctures by smashing stomatopods.

Predatory activity of decapod crustaceans is not clearly documented by traces among the investigated shelly community. It has been pointed out, that predation by crustaceans was quite subordinated in the Early Sarmatian (HARZHAUSER & KOWALKE 2002). Decapod crustaceans were represented by nearly 120 species in the previous Badenian (MÜLLER 1984), but the diversity was strongly reduced at the Badenian/Sarmatian boundary.

		test distributions (sig.)				test result
		uniform	normal	poisson	exponential	
Hydrobia frauenfeldi						
	Weighed number of drill-hole (drilling density)					
	direction	0.672	0.950	0.275	0.276	not uniform
	whorl	0.491	0.800	0.022	0.897	not uniform
	sector	0.017	0.507	-	0.099	not uniform
Weighed number of successful drill-hole (drilling density)	direction	0.312	0.898	0.270	0.185	not uniform
	whorl	0.281	0.679	0.022	0.964	not uniform
	sector	0.059	0.545	-	0.123	not uniform
Mohrensternia						
	Weighed number of drill-hole (drilling density)					
	direction	0.900	0.997	0.997	0.225	
	whorl	0.551	0.817	0.191	0.356	not uniform
	sector	0.063	0.650	-	0	not uniform
Weighed number of successful drill-hole (drilling density)	direction	0.270	0.931	0.966	0.265	not uniform
	whorl	0.456	0.900	-	0.408	not uniform
	sector	0.003	0.299	-	0	
Potamides gamlitzensis						
	Weighed number of drill-hole (drilling density)					
	direction	0.876	0.988	0.270	0.699	
	whorl	0.554	0.963	0.201	0.880	not uniform
	sector	0.041	0.551	-	0	not uniform
Weighed number of successful drill-hole (drilling density)	direction	0.458	0.924	0.270	0.636	not uniform
	whorl	0.964	1.000	0.281	0.872	
	sector	0.06	0.613	-	0	not uniform

Table 2. Testing site-selectiveness: significance values of Kolmogorov Smirnov test for different test distributions on different whorls, directions and sectors for the 3 major prey taxa (for detailed explanation on values see text)

2. táblázat. A helyválasztási stratégia vizsgálata eloszlásvizsgálattal: a táblázatban a Kolmogorov-Szmirnov próba taxononkénti és szektoronkénti szignifikancia értékei különböző eloszlásokra tesztelve

Conclusions

Summarising the results, it can be concluded, that the distribution of drillings in the Early Sarmatian endemic epifaunal gastropod community was uneven for the three main prey taxa contrary to the hypothesis. *Potamides gamlitzensis* can be considered the most common prey in the community. The attacker often avoided the *Neritina picta* and hardly ever attacked *Acteocina lajonkairieana*. In the examined material, the dominant

gastropod predator in the western periphery of the Paratethys could be the survived epibenthic Muricid after the Badenian/Sarmatian extinction. However, the shape (the observed drill-holes on the Sarmatian epibenthic gastropod community show variety from nearly perfect circle to ellipsoid) and the location of drill-holes is versatile contrary to the assumption that only a Muricid predator could cause these deformations. Other circumstances suppose the abundance of Polychaeta worms and probably *Acteocina* species as possible

attackers. Results also show that site-selection is clearly observable. The most common chosen area in prey shells is the fifth sector, which at angles 0°-90° on the second

whorl. These drill-holes cannot be connected unambiguously to the activity of worms.

Crustacean predation cannot be excluded, however it can be stated, that crustacean activity was subordinate.

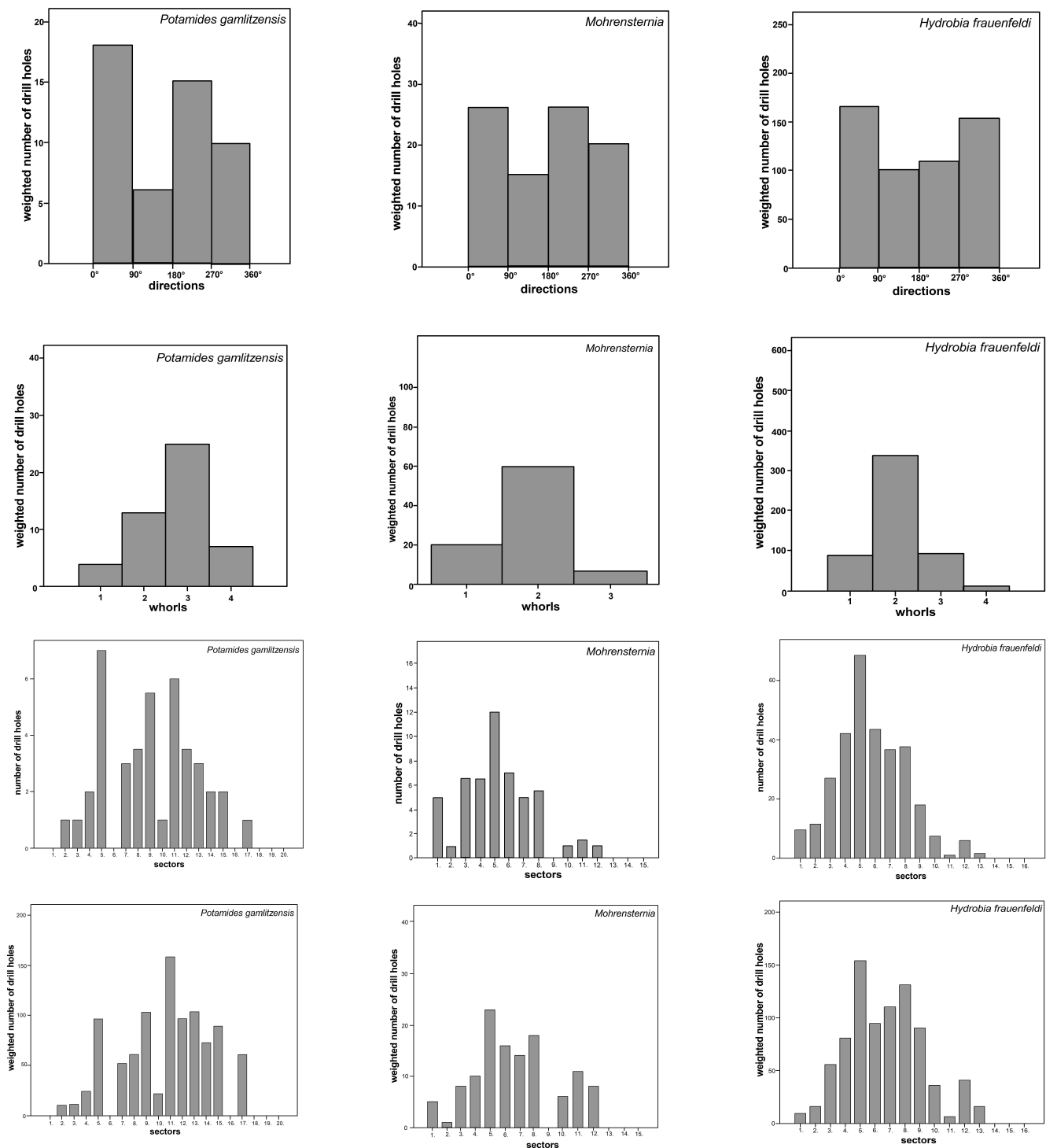


Table 3. Histograms with respect to the distribution of drill-holes
3. táblázat. A fúrásnyomok eloszlása szektoronként a 3 vizsgált taxonon

Direction/Whorl	I	II	III	IV	V
0-90	1	5	9	13	17
90-180	2	6	10	14	18
180-270	3	7	11	15	19
270-360	4	8	12	16	20

Arguments pro and contra regarding different possible attackers and predators					
Ocenebra striata +	Ocenebra striata –	worms +	worms –	Acteocina lajonkariensis +	Acteocina lajonkariensis –
<ul style="list-style-type: none"> – multiple drillings occur, referring to the probable activity of Muricids – Papp, A. describes <i>Ocenebra</i> sp. from the same sample area – epibenthic predators as the prey organisms – drillings with cylindric shape occur – abiotic circumstances do not exclude the presence of this species 	<ul style="list-style-type: none"> – prey size often too small (3-5 mms) – no fossil record of Muricids in our sample – percentage of drillings (20-26 %) on apertura 	<ul style="list-style-type: none"> – Jekelius describes similar drillings on similar Early Sarmatian community – drillings often have cylindric shape 	<ul style="list-style-type: none"> – drillings on the 1st whorl (around the apertura) are subordinated 	<ul style="list-style-type: none"> – 3rd possible predatory gastropod beside <i>Ocenebra striata</i> (Muricidae) and <i>Euspira helicina</i> (Naticidae) – only 1 drill out of 590 specimens – size of the Foraminiferae (probable prey) is reduced, low cost effectivity of predation – the extinction rate of Foraminiferae was great 	<ul style="list-style-type: none"> – probably feeds on Foraminiferae (based on recent analogies)

Table 4. Arguments pro and contra regarding different possible attackers and predators
4. táblázat. Érvek és ellenérvek a fúrásnyomok lehetséges okozói mellett

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